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SHELL MORPHOLOGY IN THE LARVAL AND POSTLARVAL STAGES OF THE SEA SCALLOP, *Placopecten magellanicus* (Gmelin)

BY ARTHUR S. MERRILL

WITH THREE PLATES

CAMBRIDGE, MASS., U.S.A.
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Bulletin of the Museum of Comparative Zoology
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No. 1 — *Shell Morphology in the Larval and Postlarval Stages of the Sea Scallop, Placopecten magellanicus* (Gmelin)

By Arthur S. Merrill[1]

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INTRODUCTION AND ACKNOWLEDGMENTS

The larval and postlarval stages of many species of pelecypods have been studied and reported by various investigators over the years. Stafford (1912) and Sullivan (1948), working with species from the northeast coast of North America, have contributed materially to our knowledge of several species. However, the sea scallop, *Placopecten magellanicus* (Gmelin), has received very little attention. Sullivan's study did not include the species, and Stafford only devoted half a page to it. Consequently, efforts to identify the early stages of the sea scallop by means of the existing literature have met with little success.

Attempts at rearing larvae of the sea scallop have also been unsuccessful (Drew, 1906; Posgay, 1953; Baird, 1953). Therefore, it has been necessary to compare the changes and modifications through an extensive series of specimens in order to identify the early stages of the species with certainty.

There is evidence that past investigators have experienced difficulty in identifying the young of the sea scallop. Dall (1898, p. 726) lists an excellent synonymy which includes several specific names thought to be new species but which later were found to be young sea scallops.

The primary purpose of this paper is to describe and figure

[1] U. S. Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, Massachusetts.

development of shell characters through the early stages of this commercially important species with the hope that it will allow future workers to quickly and accurately identify it at any stage of growth. Descriptions of the adult stage are included when it is necessary to describe later development of a particular character.

Little has been written of the early life history of the sea scallop. Jackson (1890) described and figured specimens he thought to be young *P. magellanicus* but which proved to be *Cyclopecten nanus,* a species subsequently described and figured by Verrill in 1897 (see Merrill, 1959). Drew (1906) fully described and figured both the shell and the animal of the adult, but his attempts to rear the young were unsuccessful and he was only able to discuss and figure the very early stages of embryogeny covering the first 5 days after fertilization. Stafford (1912) was able to identify *Pecten* larvae found in the plankton collected in his area but I am not convinced he could identify them with certainty below generic rank. His last paragraph about scallops on page 239 is ambiguous. If I interpret correctly, he ends his discussion by concluding that the *P. magellanicus* in his figure 35 is *Pecten islandicus.* In any case, he based his identity of allied species of *Pecten* on the differences in size of the settling larvae, but others (Jörgensen, 1946; Sullivan, 1948; Loosanoff and Davis, 1950) have found larval size to be quite variable within a species. My own observations agree with this. Morse (1919, p. 152, fig. C) does little more than figure, without measurements, the general outlines of an early stage of the sea scallop. The figure, as he says, resembles certain avicular forms. Borden (1928) gives measurements of pecten larvae, all under 0.2 mm., taken from plankton tows. However, her description of the larval form at about 0.3 mm. is incorrect, which suggests that the still younger larval forms under 0.2 mm. may not have been correctly identified. Baird (1953) published an interesting paper on the finding of a large number of tiny sea scallops on Bryozoa. However, his work is not descriptive; rather, he discusses the unsuccessful laboratory attempts to rear sea scallops beyond the trochophore stage and relates his findings to age and growth in small scallops. The present author (Merrill, 1959) described and compared the juvenile sea scallop with a somewhat similar appearing species, *Cyclopecten nanus* Verrill, but found it beyond the scope of that paper to describe and figure the various early stages of shell morphology in the sea scallop.

The material used in this study came from several sources. Sea scallops were reared in this laboratory at Woods Hole, Massachusetts, through the straight-hinge stage. A large sample of minute sea scallops was collected from a navigation buoy brought in to the Coast Guard Station at Woods Hole, Massachusetts, in June 1958. Nearly 10,000 of these tiny shells were measured, of which 80 per cent were under 4 mm., the smallest 0.5 mm., the largest 13.2 mm. Several samples were taken from other buoys as well as from the ocean bottom during the year 1958. In these samples, sea scallops as small as 0.25 mm. were collected. This is about the size at spatfall when the scallops are undergoing metamorphosis. Samples of large sea scallops taken from various stations along the coast were also available for study. The author also had ample opportunity to observe and compare the structures and variations not only in these but in other small scallops accumulated over the years from several sources by personnel of the Bureau of Commercial Fisheries, Biological Laboratory, at Woods Hole, Massachusetts.

The methods used in cleaning the minute completed larval shells, and in separating and mounting the valves are those described by Rees (1950, p. 75).

The term *height* refers to the distance from the umbo to the ventral margin; *length* to the distance from the anterior to the posterior edge (see Fig 1).

Acknowledgments are due the following individuals without whose help and cooperation the value of this work would have been considerably lessened. To Mr. Julius A. Posgay and Doctors Robert L. Edwards and Roland L. Wigley of the Bureau of Commercial Fisheries, Biological Laboratory, at Woods Hole, Massachusetts, and to Doctors William J. Clench and Ruth D. Turner and Mr. Robert Robertson of the Mollusk Department in the Museum of Comparative Zoology at Harvard University, I am greatly indebted for advice and comments after reading the manuscript. To Mr. Robert Brigham, staff photographer of the Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, and Mr. Frank White, staff photographer in the Biological Laboratories at Harvard University, I owe much for the quality of the photographs reproduced herein. I am also grateful to Mr. Frank Bailey of the Bureau of Commercial Fisheries, Biological Laboratory, at Woods Hole for the excellent line drawings.

THE LARVAL SHELL

A prodissoconch or first-formed larval shell, strikingly different from the succeeding dissoconch, is easily seen in young post-larval specimens of *P. magellanicus* (Pl. 2, fig. 1). The prodissoconch is distinctly separated from the dissoconch by a sharp line. This heavy concentric line denotes the end of the free-swimming pelagic period of the tiny scallop.

The larval development is usually divided into two stages. The first is the "straight-hinge stage" in which the veliger produces the embryonic "D-shaped" shell. This is followed by the "umbo stage" in which the shape, texture, and hinge structure are sufficiently differentiated to allow identification.

The straight-hinge larva of the sea scallop is similar to that of other lamellibranchs. It has a wide hinge-line, is relatively long in proportion to its height, and is almost equally rounded at both ends (Pl. 1). The two valves are hinged dorsally, the margins meeting ventrally and laterally. The minuteness of the shell, its transparency, and lack of structure leave few characters of importance to aid in identification at this early stage. Both valves are similar in size, shape, and curvature. They are fairly flat, and lack color. The hinge-line is usually straight, but in occasional specimens, it curves inward slightly. The size ranges from 60 to 80 microns in height and 80 to 115 microns in length in 7-day-old laboratory-reared specimens.

At the umbo stage, as seen in the completed prodissoconch, the valves are discoidal, inflated, and nearly equal in size, shape and curvature, the upper valve being slightly more convex. The structure of both valves is homogeneous, opaque, non-prismatic, and with exceedingly fine lines of growth etching the surface. The anterior end slopes somewhat more steeply than the posterior end causing the curvature to appear broadly rounded in the ventro-posterior region. The hinge-line is rather wide and straight. The provinculum is thin, raised, and lined with two rows of indistinct, minute, transverse tooth-like projections which fade and disappear on each side at some distance from the resilium (Fig. 1). The umbos are elevated, subconical, and while occupying the mid-dorsal portion of the valves, slant rearward to overlie the hinge-line. The left umbo is the more prominent. The size

(height) ranges from 0.22 to 0.32 mm. at the completion of the prodissoconch. The color is pale yellow to flaxen.

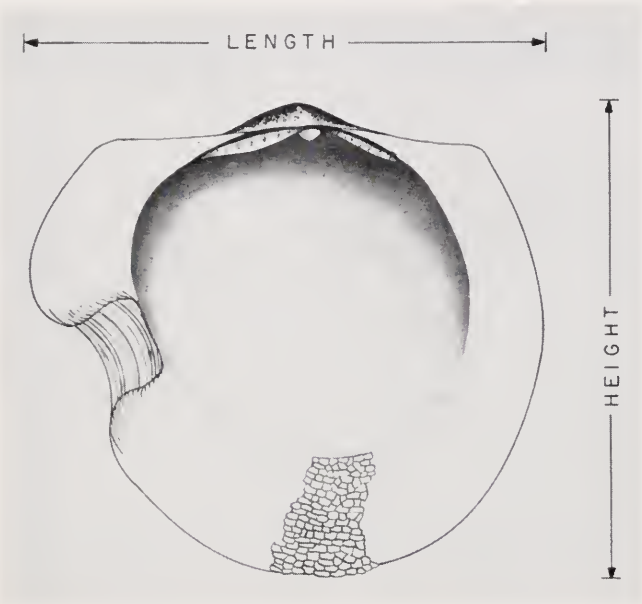

Figure 1. Line drawing of right valve showing dissoconch structure. Internal view. Height 0.5 mm.

THE POSTLARVAL SHELL

The changeover from a planktotrophic larval existence to a more or less stationary juvenile and adult life necessitates marked changes in the anatomy and shell formation of the sea scallop. These changes, modifications, and additions in the form and structure as seen at various stages in the progressive development of the shell can be brought out more clearly by a systematic description of each major character.

Shape and Color. The valves soon lose the equal convexity of the larval form, the top valve retaining a similar convexity while the bottom valve flattens considerably. The margins meet evenly until the young postlarval stages reach about 5 mm. in height when the valves begin to gape slightly but noticeably at each end in the dorso-lateral region. The gaping increases with size and is quite pronounced in adult specimens. The ventral margin is thin and simple with the upper valve slightly overlapping in

young specimens (Fig. 2). This feature remains constant during development except in some old specimens in which the edge thickens.

Figure 2. Line drawing of a specimen 17.2 mm. to show various structures of the shell in cross-section.

The form of the shell changes with growth. The prodissoconch is broadly rounded, slightly longer than high. The scallop continues to be slightly compressed dorso-ventrally until it reaches a size of 1 to 1.5 mm. at which time the height and length are about equal. The shell now gradually becomes more and more compressed laterally so that it is at its greatest extent in specimens between 70 and 90 mm. in height. Then the shell slowly begins to broaden again, and specimens 110 to 120 mm. assume a broadly rounded shape of similar height and length. The broadening of the shell continues and, in an average series, specimens larger than 120 mm. become increasingly longer than high. Individual specimens sometimes vary considerably but the measurements in Table 1 typify the general average of the sea scallop.

Table 1 — Ratios of height to length illustrating the changes in shell symmetry during growth

Height (mm.)		Length (mm.)	Ratio	Height (mm.)		Length (mm.)	Ratio
*0.072	x	0.088	1.22	78.3	x	73.1	0.93
**0.30	x	0.32	1.07	96.5	x	92.5	0.96
0.55	x	0.57	1.04	112.2	x	112.2	1.00
1.32	x	1.32	1.00	122.0	x	124.2	1.02
2.30	x	2.16	0.94	140.8	x	146.4	1.04
10.0	x	9.2	0.92	178.0	x	188.0	1.06
58.1	x	52.8	0.91	***208.0	x	230.0	1.11

*Straight-hinge veliger
**Completed dissoconch
***Largest scallop recorded in the literature (See Norton 1931)

Color pigment is lacking in the early dissoconch but when it reaches about 1.5 mm. a light cream tint develops. From this size on, color of various intensities ranging from light brown to dark reddish brown becomes increasingly prominent. Occasionally, albino, yellow, lavender, or radially dark- and light-rayed specimens are produced. Sometimes the color changes as the shell increases in size. Brown or reddish brown is the usual adult color. The under valve usually remains white or cream-colored throughout growth.

Shell Structure. The prodissoconch is thin and hyaline and continues translucent through the first few millimeters of growth of the postlarval shell. There is a complete change in the structure of the shell of the dissoconch. The larval shell with its high cuticular content is succeeded by the postlarval shell containing a high percentage of calcium salts. The shell is no longer simple; rather it becomes layered and more complex in structure.

As is well known, the periostracum, shell and ligament are products of secretion from the mantle. Outer and inner shell layers are formed in the dissoconch of *Placopecten* with color pigment being deposited in the outer layer. The periostracum and the outer shell layer are secreted by the lobes of the mantle edge with a resulting increment at the periphery. The general surface of the mantle is responsible for the secretion of the inner layer, the amount and regularity of which subsequently determines the shell thickness. The layers begin to form from the moment dissoconch growth commences. An additional layer, different in structure and composition, is formed by the modified mantle epithelium of the adductor muscle. This layer is seen to fracture on a vertical plane with respect to the shell surface. It is difficult to make out any microscopic features in this layer without using special techniques because of the homogeneity and transparency of the substance. In *Pecten*, according to Böggild (1930), this layer is prismatic in structure and the prisms are very thin, straight, regular, and oriented to a vertical axis. Böggild found (using certain techniques of refraction) that this layer is aragonitic as opposed to the calcitic outer and inner layers. The layer is first apparent in the sea scallop at about 2 mm. The outer layer is thin and only clearly visible in sectioned shells 15 mm. or less in size while the inner layer is much thicker and can be seen in all sizes. The inner layer is built up of irregular parallel leaves to appear as a foliated structure.

Figure 2 shows a transverse section of a juvenile sea scallop

of 17.2 mm., drawn with the aid of a camera lucida. Of interest is the relative thickness of the valves, the amount of overlap of the upper valve at the ventral margin, the position of the upper and lower muscle scars, and the arrangement of the hinge and ligament. Of particular interest is the method of development of the layer produced by the muscle epithelium. The adductor muscle must necessarily change position as the shell enlarges in order to maintain a somewhat central location. This is accomplished by a ventral migration of the muscle. At the same time deposition of shell material continues in the area contiguent to the muscle so that in time a distinct middle layer dorsal to the muscle is produced.

A well-defined prismatic layer is easily seen in the lower valve of the young dissoconch when viewed from above (Figs. 1 and 3; Pl. 2, fig. 2). The prisms are irregularly shaped and are secreted

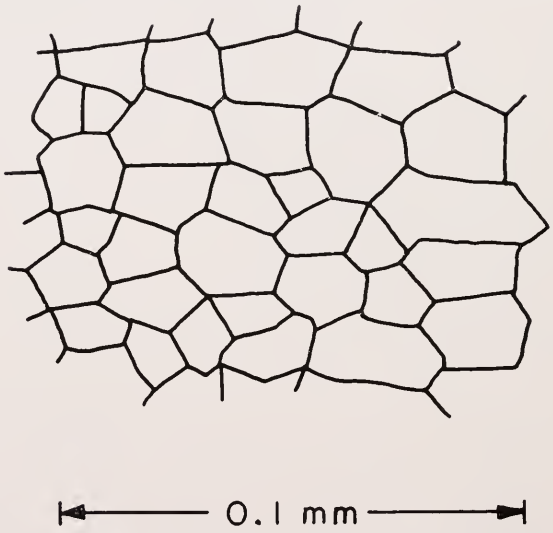

Figure 3. Line drawing to show prismatic structure in the right valve.

in an erratic, though concentric pattern. On the average, when measured near and parallel to the ventral margin, there are about 5 prisms per 0.1 mm. The prismatic pattern persists until the shell reaches about 5 to 7 mm. in height at which size the shell becomes too thick for this structure to be seen clearly.

The External Sculpture. The surface sculpture differs in the

two valves. In the upper valve, commencing with the onset of dissoconch growth, microscopic radial ridges develop which are crossed at intervals by similarly delicate concentric ridges which result in a sharply defined cancellated or nodulated sculpture. At about 2 or 3 mm. the concentric ridges weaken and gradually disappear whereas the fine radial ridges are retained. Shortly thereafter heavier raised primary ribs begin to radiate regularly among the intervening microscopic ridges which in turn fade and cease to be produced in juvenile specimens between 10 and 20 mm. The fine ridges may be straight and regular or they may be vermicular or oblique in which case they usually cross the ribs. This is the "camptonectes" sculpture of Verrill (1897). Commencing with the juvenile, the regularly spaced primary ribs are a prominent part of the upper valve, new ribs being added between them as the shell enlarges (Pl. 3). When they first appear, the ribs are spaced about 0.3 mm. apart. When the spacing increases to 0.8 to 1.2 mm., a new rib is added. The distance between the ribs increases as the shell size increases until in the adult stage the ribs are spaced about 1 mm. apart. The ribs of the adult may be strongly raised and serrated causing the shell to look and feel rough, or, in the case of a smooth-shelled adult, the ribs may be but slightly raised.

Any concentric markings beyond that mentioned for the early dissoconch are in the form of numerous fine laminal lines (striae) as the result of frequent additions during growth. At intervals these lines of growth become more closely spaced appearing as thickened bands of shell material. Stevenson and Dickie (1954) and most present-day investigators working with the sea scallop believe that the more prominent bands are caused by the seasonal changes of growth pattern, as has been demonstrated with the annual rings of trees or fish scales.

Radial sculpture is formed somewhat similarly in the bottom valve. However, due to the formation of prismatic structure in the early dissoconch the fine ridges do not start forming until the shell is about 5 to 7 mm. in height. Primary ribs soon develop as in the upper valve but not as strongly. Although both the ribs and ridges usually persist through to the adult, either or both may disappear during the course of development. If the sculpture persists it is weaker than in the upper valve.

The radial sculpture of the wings is similar to that on the surface of the shell, but it is usually more strongly developed, especially so in the anterior wings (Pl. 3). Concentric sculpture

ending at the wing margins forms crenulations at the hinge line.

The Inner Shell Surface. The mantle is attached to the shell by a series of muscles along the pallial line. The mantle is able to expand and retract from this line to the outer edge of the shell. In the adult the surface area outside the pallial line appears smooth and lustrous to the eye but upon closer examination flakey laminal

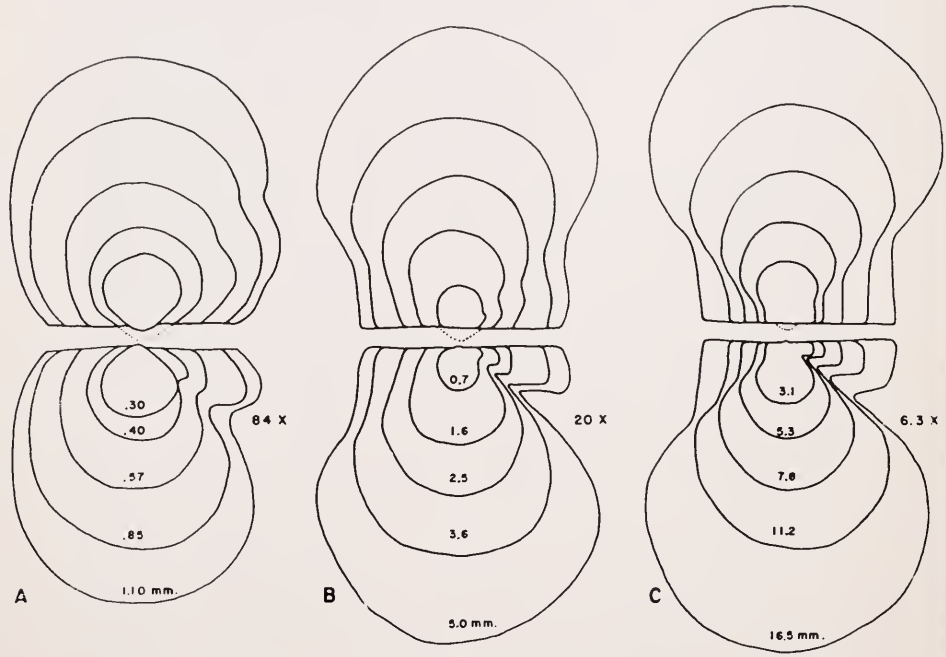

Figure 4. A series of line drawings showing the development of the wings of the sea scallop.

layering can be observed, particularly near the margin. Also, very fine lines radiate to the margin. Within the pallial line, the calcium deposits appear nacreous with coarse and irregular layering. The adductor muscle scar is large, distinct, and, particularly on the right valve, placed off center toward the posterior border. The scar on the left (upper) valve is the larger and there is a line showing the separation of the muscle into a large anterior and a small posterior part. Within the scar, lines denoting the attachment of individual bundles are evident. The adductor muscle is attached to the valves somewhat more dorsally

and posteriorly in the young especially in the right valve, but it gradually moves to a more central location with increase in shell size, and after about 50 mm. advances proportionally to the ventral margin of the shell. The muscle scar forms a slight depression and is surrounded by the crystalline substance. The peculiar crystalline structure within the pallial line is first evident in the upper valve at about 2 mm. but soon can also be seen in the thinner bottom valve.

The Auricles or Wings. Figure 4 compares the outline of specimens in a series ranging in size from 0.3 to 16.5 mm. in height. These were specifically drawn to show the development of the wings. As can be seen, the settled prodissoconch lacks them. The earliest indication of their development appears in specimens which have put on just a fraction of a millimeter of dissoconch growth. A notch develops in the lower valve at the anterior margin, the portion of the newly-formed shell dorsal to the notch consequently appearing ear-like. The wing becomes broadly rounded as the height increases to about 2 mm. It now begins to angulate (Fig. 4b) and continues until the shell is about 10 mm. in height when the angle again broadens (Fig. 4c). The angle becomes less acute as the shell size increases so that in the adult this wing is more nearly symmetrical with the posterior one.

The development of the anterior wing in the upper valve proceeds in a peculiar fashion. A rounded flap begins to develop almost immediately, projecting over and overlying the byssal notch. Although fully developed at 1 mm., it persists through growth to nearly 5 mm.

At the same time as these wing-like processes are developing, slight indentations or depressions begin to form between them and the body wall. These are the slopes or submargins, the points where the wings can be distinguished from the body proper.

The posterior wings begin to develop at about 2 mm. and, with increase in size, slowly become more strongly outlined as the posterior submargins strengthen. The wings are easily distinguishable before 5 mm., becoming even better developed as the shell size increases. However, it is interesting to note that the ears are proportionally smaller in larger specimens. At 2 mm. the width of the hinge-line is about four-fifths the length of the shell, at about 35 mm. only about one half, and thereafter very gradually decreasing. The shell measurements in Table 2 clearly show this characteristic.

Table 2 — Width of hinge-line compared to length showing the decrease in the wing width in relation to length with growth (in millimeters)

Height	Length	Width of hinge-line	$\frac{\text{Width of Hinge-line}}{\text{Length}} \times 100$
1.9	1.8	1.5	83.3
5.8	5.2	3.8	73.1
10.5	9.1	6.3	69.2
21.3	18.9	11.6	61.4
34.6	31.6	16.2	51.3
52.3	48.0	20.8	43.3
106.8	104.2	44.3	42.5
142.6	147.7	62.0	42.0

Hinge-Plate. In young specimens the hinge-plate is thin, raised, and with a simple ligamental groove below the margin which is separated by an internal resilium (Fig. 5). The indistinct transverse teeth present in the prodissoconch cease to develop in the

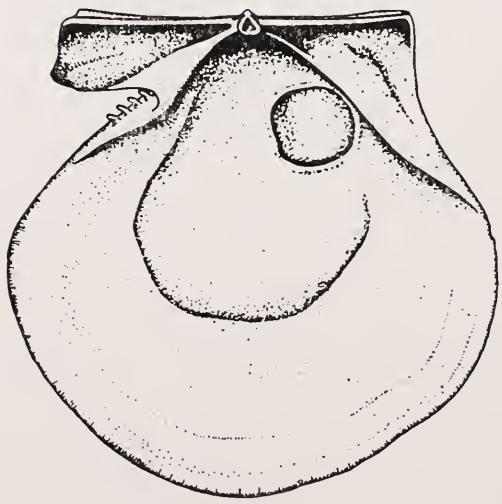

Figure 5. Line drawing of right valve of a specimen 5.7 mm. showing hinge-line and other internal characters.

early dissoconch. As the hinge-line develops, deposition of new material obliterates the larval teeth at about 0.5 mm. The hinge-plate, only slightly differentiated in the very young, becomes increasingly raised along the exterior margin as the shell develops

and this is directly responsible for the greater gaping of the valves in the dorsolateral region. At the hinge-line, the exterior margin is crenulated and recurves inward to impinge on the hinge-plate and partly overlap the ligamental groove. This becomes more apparent with increased shell size.

The Byssal Notch. Formation of the byssal notch commences at the moment of dissoconch growth. In the early dissoconch, little shell material is deposited in the lateral region of the under valve where the notch is located; instead, a rounded indentation is produced. With increase in size the notch advances accordingly as shell material is deposited behind it (Fig. 1). This material is not prismatic as is the rest of the valve in the early dissoconch; rather it appears homogeneous and hyaline, with laminated, concentric growth lines running parallel to the notch. As the shell enlarges and the notch continues to advance, a ridge is produced along the anterior submargin above which a groove has been excavated. A number of pectinidial teeth develop along the ridge. Teeth begin to form at a size of about 1.5 mm. (Pl. 2, fig. 2) and cease after about 25 mm. Occasionally, the teeth are feeble or may not develop at all. In one specimen over 30 teeth were counted. Plate 3, figure 1 illustrates a 5.7 mm. specimen in which 15 teeth are present. The early-formed teeth can usually be observed in the adult well back on the raised ridge in the vicinity of the umbonal region unless erosion or calcification has destroyed or covered them. The notch is broad and rounded inside for the first millimeter or two (Fig. 1) but soon begins to angulate as the wing develops. After a size of 10-15 mm. the angle becomes gradually less acute (Pl. 3, fig. 3) as the notch fills in so that in the adult the notch is almost entirely obliterated.

The Ligament. The structure, function and mechanical properties of the ligament in *Pecten* have been fully described and discussed by Trueman (1953a, b). Briefly, the ligament joins the two valves of the shell together dorsally along a hinge-line and functions by working in opposition to the adductor muscle, thus forcing the valves to gape apart when the muscle is relaxed. There are two layers, the outer which extends thinly along the dorsal margin of the valve hinges, and the inner which is centered immediately below the hinge at the umbo. A thin layer of periostracum is produced over the outer layer. The layers are laminated and, according to Trueman (1953a), composed largely of tanned proteins, an organic matrix commonly referred to as "conchiolin."

The inner layer, or resilium, is triangulate in shape, its apex coincident with the umbonal point of the valves. It is housed in a depression, the resilifer, the base of which projects shelf-like into the cavity of the shell. It is composed of three parts: a large central region consisting of amorphous, non-calcareous tanned proteins, brown in color and of a rubbery consistency, and two small lateral calcified regions in the area of attachment to the resilifer.

In the early postlarval shell of the sea scallop the outer ligament lines the hinge as a very thin, transparent substance. As the shell enlarges this layer becomes increasingly conspicuous principally because the brown color in it is darker.

In the larval shell of *Pecten* the ligament is situated internally and off center on the straight hinge toward the posterior broad end of the larva (Rees, 1950). In the recently settled larva of the sea scallop the resilium is about centered between the umbos (Fig. 1). It is wide and rounded, and seated within a weakly developed resilifer. After the first millimeter of growth the resilium begins to lengthen and soon takes an almost equal-sided pyramidal shape as new ligamental material is added ventrally and laterally. After 5 mm. (Fig. 5) to 10 mm. the resilium gradually begins to elongate in a dorso-ventral direction until in the adult it is long and slender. The resilifer strengthens with growth, the depression gradually deepening so that in the adult the resilium is deeply rooted.

The ligament, formed by secretions from the mantle, is subject to the same general growth and shock lines as is the shell. Less prominent impressions are found in the tanned protein portion than in the calcified outer portion of the inner ligament.

DISCUSSION

The major changes during the development of the shell of the sea scallop have been described in the preceding pages, thus serving the primary purpose of this paper. However, the subject would not be complete without a brief discussion of certain points described elsewhere.

The D-shaped veliger shell is usually distinctly marked off from the umbo veliger stage in most species (Rees 1950). This is not the case with the sea scallop. Apparently there is little or no cessation of growth during larval shell development to cause this distinct line to be formed. Thus, the early veliger is almost impossible to identify in the plankton. Also the size at this stage

varies considerably and is of little use as a character. This agrees with Jörgensen's (1946) findings regarding the reliability of the length of Prodissoconch I ["straight-hinge" stage] as a specific criterion. Of course, by the time of development to the umbo stage this species should be identifiable through hinge characters. Stafford (1912) states that larval sea scallops are easily identified because of their equal measurements in length and depth. Of the scallops examined in this study, the length commonly exceeded the height in the prodissoconch. Stafford also speaks of a notch that may appear in front of the median point of the margin, which soon develops into two little beaks on the left valve, and a larger interlocking tooth on the right valve. Borden (1928) also remarks on this occurrence but it is quite possible she simply followed Stafford's earlier work. No such anomiaiid-like character was observed in any of my specimens. In fact, I should be very much surprised if such a character existed in this species, principally because it is not a known phylogenetic character in the Pectinidae.

The prismatic structure in the under valve of the early post-larval sea scallop has been described elsewhere in this paper. In very young specimens the margin of this valve is very thin and flexible due to the organic matrix bordering each prism. Similar prismatic structure can be seen in other species of the Pectinidae, and is especially prominent in thin-shelled deep-water forms. Carpenter (1847, p. 95) first observed this character in *Pecten nobilis*. The flexibility of the under valve allows the shells to compress snugly together when necessary and seems to serve essentially to give extra protection.

The very young sea scallop puts out a short branching byssus which allows it to adhere closely to the surface to which it attaches. The rounded flap that precedes the development of the anterior wing overlies the byssal notch and appears to function as a protective lid in the young dissoconch. Thus when a young scallop is disturbed it squeezes its valves tightly together and, being attached close to the surface with its attachment protected, is better able to withstand and survive the early vicissitudes of life.

Before leaving the subject of byssal formation, it is of interest to note that the sea scallop retains the habit of byssal fixation for some time after reaching adult size. I have measurements of scallops as large as 112 mm. in height which were found still attached to rocks. The scallop does not remain attached all of

this time. It frequently breaks away and swims about for a time before attaching again.

It should be noted that Dall (1886, pp. 207, 222) and Verrill (1897, p. 79) both described well-developed transverse incisions on the hinge-plate in young sea scallops as did Jackson (1890). I have not been able to detect any signs of transverse grooves or ridges in this species other than the very indistinct transverse tooth-like projections in the larval shell which fade and disappear very shortly in the dissoconch and which are invisible unless the specimen is properly prepared and mounted. Apparently the above authors, like Jackson, had the young of other species before them when they described this feature.

Dall (1889) discusses the radiating ridges or ribs found in certain groups of pelecypods and concludes that they serve to add strength to the shell while not increasing the weight as would a corresponding increase in thickness of the shell. As it happens, the adult sea scallop increases the thickness of the shell rather than develop strong radial sculpture. However, the young scallop of 5 to 30 mm. (Pl. 3) has rather strong ribs which would tend to strengthen the shell before it has had a chance to thicken markedly. The radiating ribbed sculpture of the wings is particularly strong. The wings at these sizes are proportionally wider at this early age but thin, and the extra strength is desirable in this area of the pivotal axis of the valves where there are mechanical stresses and reactions of one valve upon the other for the scallop to contend with.

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PLATES

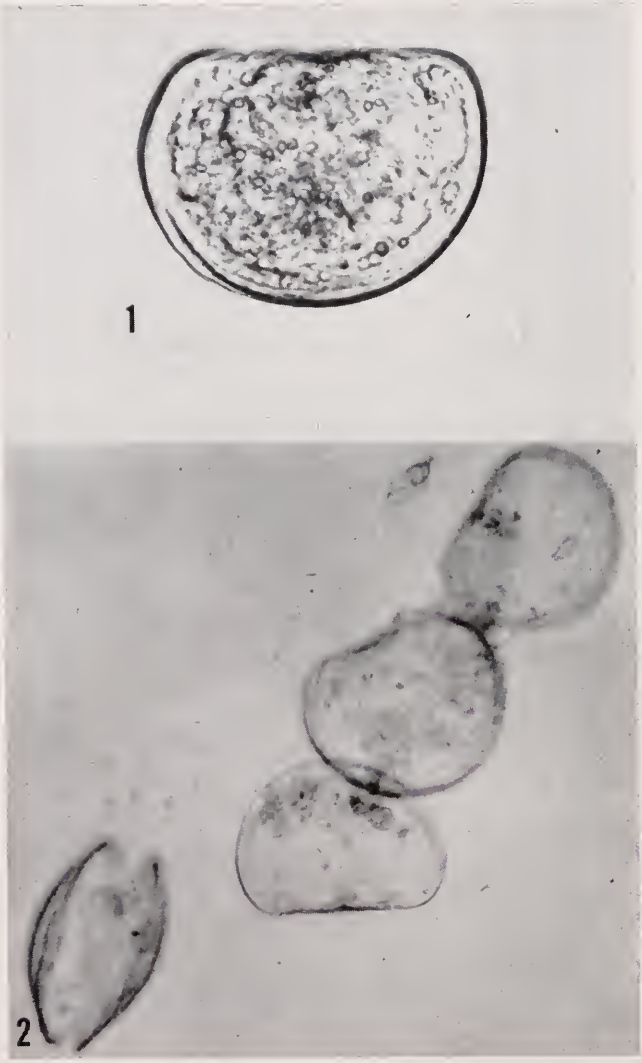

PLATE I

Figure 1. Seven-day-old laboratory-reared sea scallop in the straight hinge stage. Animal within shell (about 300X).

Figure 2. Same as Figure 1. Shell valves only (about 500X).

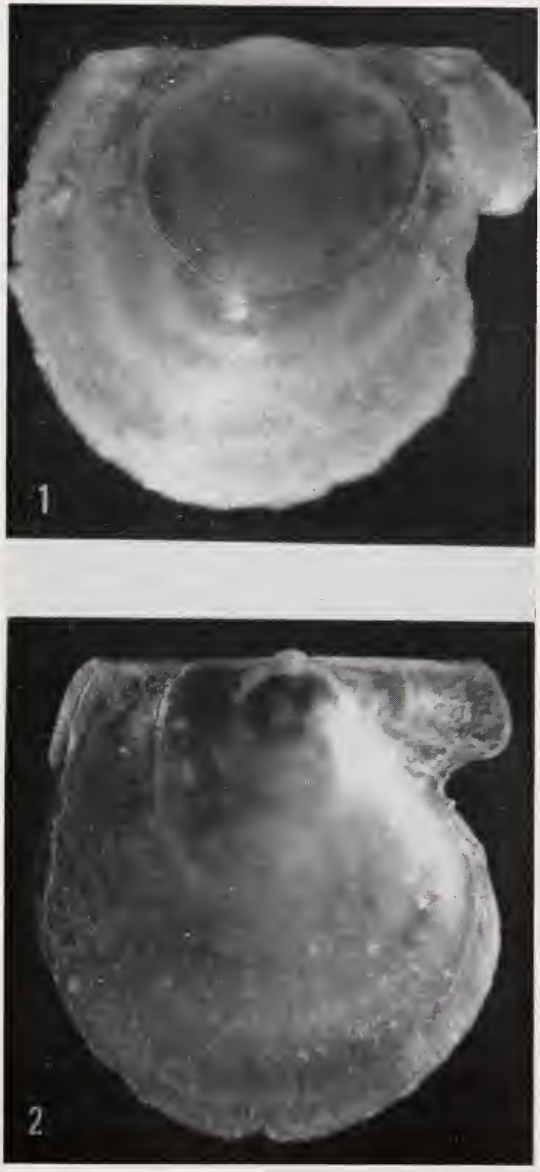

PLATE 2

Figure 1. Right (bottom) valve of early postlarval sea scallop. Height 0.5 mm.

Figure 2. Right valve showing first pectinidial tooth. Height 1.5 mm.

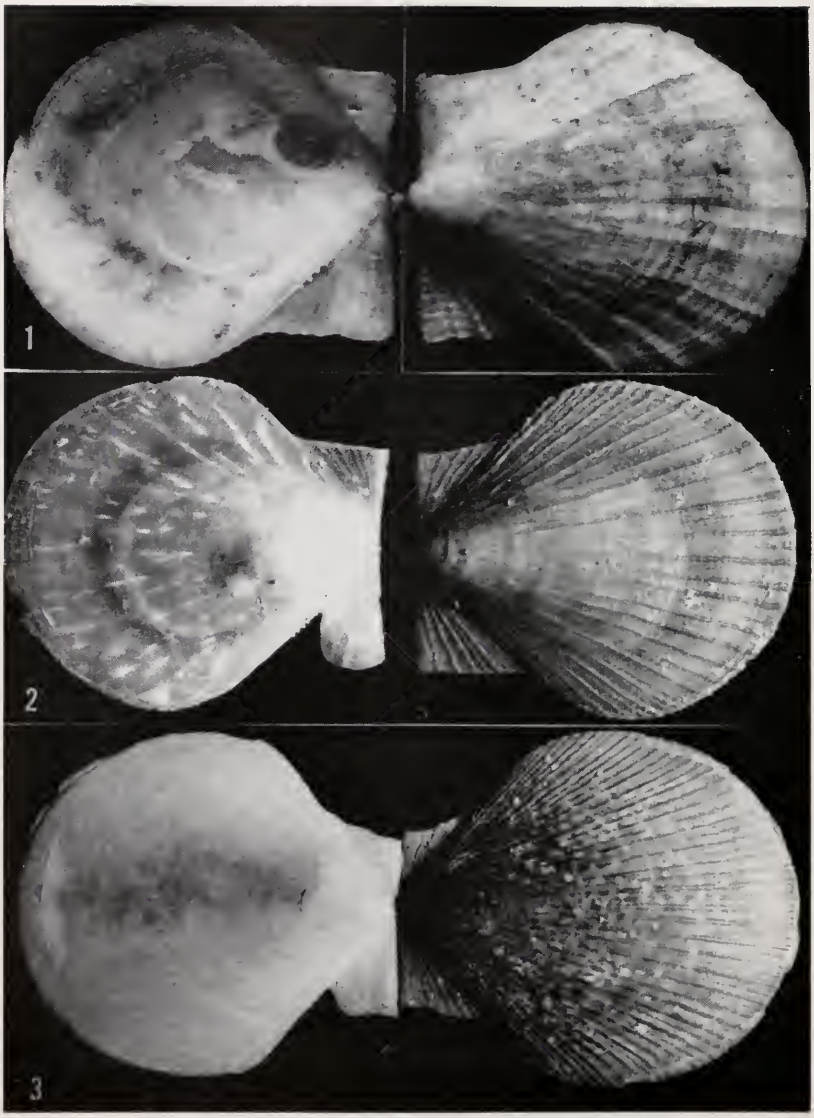

PLATE 3

Figure 1. Left and right valve of a specimen 5.7 mm. in height (both valves doubled).

Figure 2. Left and right valve of a specimen 11.7 mm. in height.

Figure 3. Left and right valve of a specimen 20.5 mm. in height.

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ON THE MAJOR ARTERIAL CANALS IN THE EAR-REGION OF TESTUDINOID TURTLES AND THE CLASSIFICATION OF THE TESTUDINOIDEA

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No. 2 — *On the major arterial canals in the ear-region of Testudinoid Turtles and the classification of the Testudinoidea*

By Samuel Booker McDowell, Jr.

That there is an osteological difference in cranial foramina between typical emydine and testudinine turtles, on the one hand, and kinosternines (mud-turtles), on the other, has been known for some time. Siebenrock illustrated (1897, pl. 2, fig. 8) the inner view of the cranial chamber of "*Cinosternum odoratum*" (=*Sternotherus odoratus*) and showed a foramen labeled f.c.i.' ="Foramen caroticum internum, Zweig zur Augenhohle hinziehend" that does not appear in his figures of other Testudinoidea (*Chelydra serpentina*, *Testuno* (*sic*, =*Psammobates*) *tentoria*, *Cyclemys dhor* (=*C. dentata*), and *Geoemyda spinosa*). I can find no discussion in Siebenrock's text on this foramen in "*Cinosternum.*"

A more striking difference, because it is more easily observed, was still earlier noted by Baur (1888b), who found that an arterial foramen between the pro-otic and quadrate seen in nearly all turtles is greatly reduced or absent in *Dermatemys*, *Staurotypus*, and the kinosternines. This feature was confirmed by Bienz (1895) and is cited, as one of many osteological characters, in the classification of turtles by Romer (1956).

But while this characteristic has long been known in terms of osteology, there is no work, to my knowledge, describing the difference between mud-turtles and pond-turtles in the arterial supply of the head. Since closure of a large arterial foramen implies considerable rearrangement of the head arteries, a knowledge of the arteries would seem essential to interpretation of the osteological features.

Dissection of *Kinosternon subrubrum* and *Sternotherus odoratus* (kinosternid foramen-pattern) and of *Malaclemys* (*Graptemys*) *geographica*, *Chrysemys* (*Trachemys*) *scripta*, *Chrysemys picta*, *Gopherus berlandieri*, *Testudo* (*Testudo*) *graeca*, *Ocadia sinensis*, *Chinemys reevesi*, *Clemmys insculpta*, *Emys orbicularis* (Kunkel's series F slides, Kunkel, 1912), and *Chelydra serpentina* (juvenile) (testudinid foramen pattern) convinces me that the two foramen patterns are indicative of two quite different adult arterial patterns, and further, that neither arterial pattern

can be derived directly from the other one, although both may be derived from a more generalized pattern, such as that seen in living Cheloniidae.

I. THE PATTERN OF THE TESTUDINIDAE

Bony canals and foramina: — There is an opening on the rear surface of the skull, called the posterior aperture by some authors = the foramen jugulare internum of Siebenrock (1897), the fenestra postotica of Nick (1913). This opening is bounded laterally by the quadrate, ventrally by the pterygoid, and medio-dorsally by a vertical lamina of the opisthotic or the exoccipital or the two bones together. (Since this lamina represents a posterior protection for the peculiar pericapsular extension of the perilymphatic sinus characteristic of turtles, I propose to call it the crista postperilymphatica, *new term.*) Nick's name for the opening, fenestra postotica, seems more fortunate than Siebenrock's name, foramen jugulare internum, since the opening rarely contains the strict homologue of the mammalian vena jugularis interna. Rather, it contains the main reptilian head-vein, the vena capitis lateralis, sometimes called, by analogy, the "internal jugular," but more nearly homologous to the mammalian sinus cavernosus. The turtle homologue of the mammalian vena jugularis interna is a rather small vein closely bound to the vagus nerve, and with the nerve piercing the crista postperilymphatica by an opening I here call the apertura vagi, *new term.*[1] The vein and vagus may then be followed deeper within the skull and be seen to enter the true foramen vagi or foramen jugulare between opisthotic and exoccipital. The vena jugularis interna then extends mediad in the dura mater above the brain (cf. mammalian sinus transversus) to join a longitudinal vein in the dura mater on the midline above the brain (cf. mammalian sinus sagittalis superior). In

[1]Throughout this paper in dealing with openings in the dried skull for cranial nerves, I have used the word "foramen" for holes in the primary braincase, and the word "apertura" for holes in the secondary investments of the primary braincase. This convention is particularly necessary in dealing with holes for transit of the glossopharyngeal nerve; in such turtles as *Orlitia* this nerve pierces bone three times: (1) an internal glossopharyngeal *foramen* leading from the cranial cavity into the inner ear cavity of the dried skull, (2) an external glossopharyngeal *foramen* from the inner ear capsule to the pericapsular space, and (3) a glossopharyngeal *aperture* in the crista postperilymphatica (a secondary investment of the primary braincase). The second hole is invariably present in turtles; the first is often undefined by bone in young turtles, but is probably constant for all fully mature skulls. The third hole is absent in adults of many turtles. Without a convention the name "external glossopharyngeal foramen" would be ambiguous and might refer either to the constant foramen in the posterior wall of the ear capsule or to the variable "aperture" in the crista postperilymphatica.

Platysternon the apertura vagi is not defined laterally by bone from the fenestra postotica, but is merely a deep notch, while in *Hardella* it is a rather shallow notch. In other testudinoids, however, the opening for the true internal jugular is set off by bone from the fenestra postotica.

The fenestra postotica is usually triangular in form, and we may speak of a "dorsal corner," a ventro-lateral corner," and a "ventro-medial corner." In addition, the columella auris may be seen passing across the fenestra as it extends from the fenestra ovalis to the ear-chamber in the quadrate. Thus, it is sometimes convenient to refer to a "supracolumellar portion of the fenestra postotica" and an "infracolumellar portion of the fenestra postotica." The infracolumellar portion is a rather narrow horizontal slit (for the only structures to pass here are the internal carotid artery and the chorda tympani nerve and Jacobson's and the auricular anastomotic nerves).

Deep within the skull, the supracolumellar portion of the fenestra postotica appears divided into two passageways. The smaller passageway is at the dorsal corner and leads upward and forward between the pro-otic and quadrate bones to open by a foramen into the temporal fossa. This passageway and the foramen forming its opening to the temporal fossa are, respectively, the canalis caroticus externus and foramen carotico-temporale of Siebenrock (1897), while Nick terms the opening "Foramen arteriae facialis," in accordance with a different terminology for the vessel. Actually, the foramen transmits both the temporal stem of the stapedial artery and a branch of the vena capitis lateralis. Since the homology between the stapedial artery and adult human external carotid is far from exact, the differences being in precisely this region, I modify Siebenrock's names to canalis stapediarterialis and foramen stapedio-temporale, *new terms*. While arteria facialis is sometimes used as a name for the stapedial artery of lizards, it has also been used in human anatomy in a different sense; therefore, Nick's name is avoided here.

The larger passageway from the supracolumellar portion of the fenestra postotica leads forward and mesiad to open just lateral to the notch (incisura pro-otica) in the pro-otic bone for the trigeminal ganglion. Nick's (1913) felicitous name for this passageway is canalis cavernosus, while he terms the anterior orifice the foramen cavernosum: since the chief occupant of the passageway and the foramen is that portion of the vena capitis

lateralis homologous with the cavernous sinus of human anatomy, Nick's terminology is here adopted. Essentially, however, the canalis cavernosus of turtles corresponds to the cranioquadrate space or passage of other gnathostomes; the outer wall is formed mainly by the quadrate (with some contribution from the pterygoid, particularly anteriorly), while the bony ear-capsule forms the inner wall. Thus, the facial nerve also runs through the canalis cavernosus from a foramen in the mesial wall of the canalis.

As to the infracolumellar portion of the fenestra postotica, the ventro-mesial corner of the fenestra is set off by a snag of the pterygoid as the foramen caroticum internum of Siebenrock (1897). In the present paper, I use "stapedial artery" for what Siebenrock termed the external carotid, and so "internum" becomes an unnecessary adjective. It seems desirable, however, to make a distinction between a foramen into the pituitary fossa for the carotid, a constant feature of all turtles, and this outermost opening in the skull for the carotid, an opening that shows interesting and taxonomically useful variations. I here propose the name foramen caroticum definitivum for the outermost opening in the skull for the carotid (that is, the internal carotid of many authors); for the foramen into the pituitary fossa (that is, in what ossifies as the basisphenoid) I shall use the name foramen caroticum primitivum (this terminology by analogy to that used for the foramen stylomastoideum in mammals).

The foramen caroticum definitivum leads to a canal that runs forward to the foramen caroticum primitivum. This canal is here called the canalis caroticus. The ventral wall of the canalis caroticus is formed by the pterygoid, the dorsal wall by the ear-capsule; that is, the pro-otic forms the dorsal wall anteriorly, and in *Batagur, Callagur,* and *Kachuga trivittata* the opisthotic forms a more posterior continuation of the dorsal wall (and hence, in these genera, the dorsal margin of the foramen caroticum definitivum). In *Morenia* and *Geoclemys* the pterygoid comes to surround the canalis caroticus, and the foramen caroticum definitivum is entirely in the pterygoid. The canalis caroticus gives off two small branches: a posterior branch is given off about opposite the fenestra ovalis to run forward in the pterygoid bone, usually to open onto the dorsal surface of the palate near the anterior extremity of the descending process of the parietal or just anterior to the epipterygoid bone; an anterior, usually minute

branch issues from the canalis caroticus just lateral to the foramen caroticum primitivum or forward of that point and runs forward on the dorsal surface of the pterygoid to disappear or else connect by a diagonal groove with the anterior opening of the canal for the more posterior branch. The more posterior of these canals is the Vidian canal, while the more anterior is here called the canalis arteriopalatinus.

In addition, near the foramen caroticum primitivum there may be a ventral branch of the canalis caroticus that opens onto the pharyngeal surface of the pterygoid. This is here called the canalis carotico-pharyngealis, and its ventral opening, the foramen carotico-pharyngeale. This is a conspicuous foramen in American *Clemmys, Terrapene, Emys,* and *Emydoidea,* but is small or absent in the other genera.

Arteries: The arteries in the head of *Emys orbicularis* and *Testudo* (*Testudo*) *graeca* have been described by Shindo (1914) and his findings are summarized in Hafferl (1933). Unfortunately, the few papers on head arteries of turtles have been morphological studies aimed at discovering the basic agreement between all reptiles, and at interpretation of the fate, in the adult, of the aortic arches. While these works have been invaluable in understanding the broad sweep of anatomical specialization and evolution among tetrapods, they are less helpful in understanding the details of phylogeny within one superfamily of testudinoids.

My most satisfactory dissections have been of two beautifully injected *Chrysemys* (*Trachemys*) *scripta* prepared by Champlain Biological Supply Company, to whom I bear a great debt of gratitude. Less satisfactory dissections (but adequate at least for the major arteries) have also been made of *Chelydra* (juvenile), *Rhinoclemmys pulcherrima, Ocadia, Chinemys, Testudo, Gopherus, Chrysemys picta,* and *Malaclemys* (*Graptemys*) *geographica.*

After giving off the lingual artery (external carotid of some authors, or ventral carotid) in the anterior part of the neck, the carotid stem continues forward to divide into two branches, a dorsolateral stapedial artery and a ventromedial carotid (or internal carotid). Of the two, the carotid is the smaller.

Almost immediately the stapedial artery gives off small branches to the region of the Eustachian tube, particularly to a structure characteristic of all turtles, but never, to my knowledge,

named or described: the operculum tubae, *new term*. The operculum tubae is a dense, ereseentie pad of connective tissue attached by its straight dorsal edge to the posterior extremity of the pterygoid and a roughened area of the quadrate just above the notch for the columella. The convexly rounded ventral border of the opereulum tubae hangs down as a free flap held only by loose connective tissue. This flap lies immediately behind the chorda tympani and the Eustachian tube (it is, in all likelihood, a specialization of tissue associated with the posterior wall of the Eustachian tube). The effect of this pad of connective tissue is to press the Eustachian tube closed; however, a branch of the depressor mandibulae muscle (here called the museulus dilator tubae, *new term*) runs from a crest formed by the opisthotic and supratemporal (squamosal of most authors) to the posterior surface of the operculum tubae. Contraction of the muscle draws back the opereulum and opens the Eustachian tube. Very likely this is a necessary means of opening the Eustachian tube in a skull with an immovable pterygoid bone, where kinesis of the pterygoid will no longer open and close the adjacent pharyngeal opening of the Eustachian tube. Mammals, faced with a similar problem, have solved it in a different way: by enwrapping the Eustachian tube in the swallowing muscles of the velum palatinum, they have made the act of swallowing simultaneously the act of opening the Eustachian tube by muscular massage.

The stapedial artery (arteria temporomaxillaris of Shindo) enters the fenestra postotica in a dorsolateral position, near the dorsal corner of the fenestra. Here, within the skull, between the quadrate and the bony auditory capsule, the artery divides into a dorsal and a ventral branch.

The ventral (mandibular) branch runs with the vena capitis lateralis to exit at the trigeminal aperture. It is usually minute, but large in *Testudo*, *Gopherus*, and *Rhinoclemmys*.

The dorsal (larger) branch passes through the canalis stapediarterialis and out by the foramen stapedio-temporale into the temporal fossa. It is accompanied by a small branch of the vena capitis lateralis. At the foramen stapedio-temporale the artery is divided into a posterior branch running back to the neck along the floor of the temporal fossa (arteria cervicalis of Shindo), and an anterior branch that curves upward and forward and lies in a distinct groove on the external surface of the descending process of the parietal. At about the transverse level of the foramen for

the fifth nerve (but considerably dorsal to the nerve foramen) this anterior branch becomes separated from the parietal and runs through the musculature of the temporal fossa to a point dorso-posterior to the eye; here the artery gives off branches. A small branch (supraorbital) runs above the eye to supply the upper lid and to disappear into a small foramen in the prefrontal, but the main branches (infraorbital) run downward to make contact with the branches of the trigeminal nerve. It is these branches that supply the palate and nasal chamber, essentially following the branches of the nerves. The palate is supplied by a U-shaped artery, continuous across the midline, that runs medial to the border of the triturating surface. This U-shaped artery receives blood mainly from a branch of the suborbital artery that passes through the suborbital foramen or fenestra[1] while a branch of the suborbital artery may join the U shaped artery anteriorly by passing through the nasopalatine foramen. On each side of the mid-line the U-shaped artery gives off a forward branch that enters the nasal chamber from beneath by passing through a pair of foramina (usually near the premaxillo-vomerine suture) that have been called the incisive foramina, but since the incisive foramen of mammalian anatomy is for the duct or ducts of the nasal gland and Jacobson's organ (which are not associated with the foramen of turtles), the foramen cannot be homologous in turtles and mammals. I prefer Seydel's name foramen praepalatinum for the foramen of turtles.

The carotid proper (internal carotid) enters the canalis caroticus by the foramen caroticum definitivum, in company with the auricular and Jacobson's nerves.[2] These nerves enter the Vidian canal to join with the palatine ramus of the facial nerve, forming the Vidian nerve; a branch of the carotid, here called the Vidian branch, also enters the Vidian canal to pass forward to the dorsal surface of the palate. The Vidian branch of the carotid is very small. Farther forward, the carotid may give off a small branch that passes through the canalis carotico-pharyngealis to supply the roof of the pharynx. Just lateral to the foramen caroticum primitivum a usually small artery is given off from the carotid to

[1] I term this hole "suborbital foramen" when it is completely filled by the vessels and nerves as in *Malaclemys*. When the hole in the dried skull is enlarged and mainly filled by membrane in life (e.g. *Clemmys*) I term it the "suborbital fenestra."

[2] I prefer the name "Jacobson's nerve" to "tympanic nerve" for this part of the sympathetic trunk connecting the glossopharyngeal and palatine nerves, since in turtles this nerve is remote from the tympanic cavity.

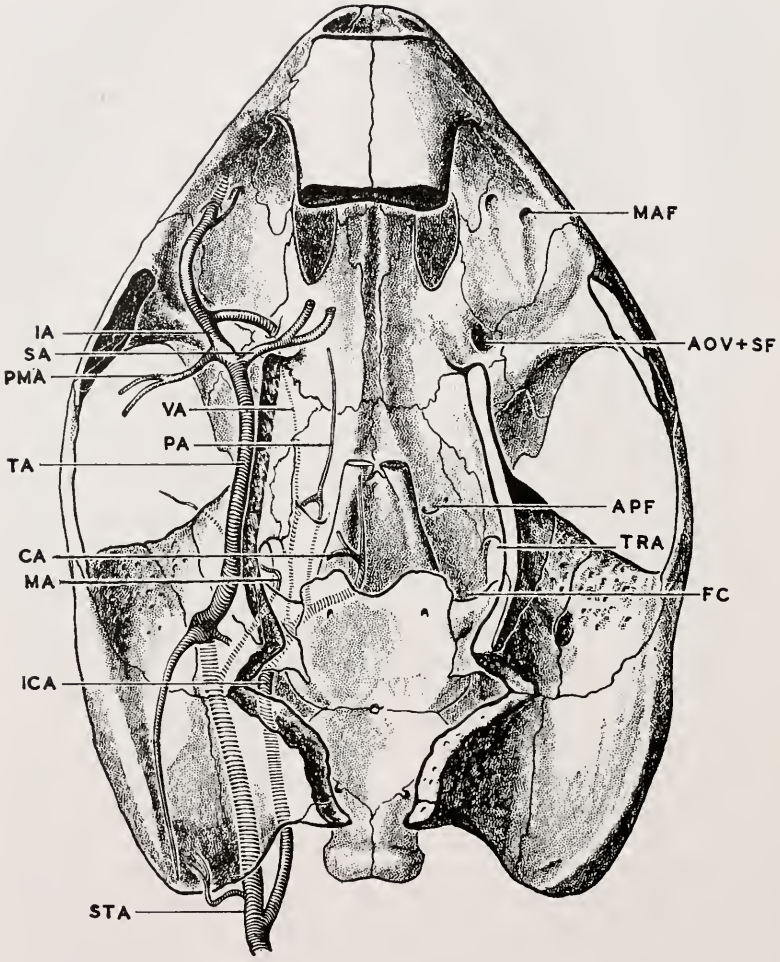

Figure 1. Dorsal view of arterial circulation (left side) and arterial foramina (right side): testudinid pattern (semidiagrammatic), based on *Malaclemys* (*Graptemys*) *geographica*. Abbreviations: AOV+SF, anterior orifice of Vidian canal and suborbital foramen; APF, foramen arteriopalatinum; CA, cerebral carotid artery; FC, foramen cavernosum; IA, infraorbital artery; ICA, (internal) carotid artery; MA, mandibular artery; MAF, maxillary arterial (alveolar?) foramen; PA, palatine artery; PMA, pseudomandibular branch of infraorbital artery; SA, supraorbital artery; STA, stapedial artery; TA, temporal portion of stapedial artery; TRA, trigeminal aperture; VA, Vidian artery.

run forward in the canalis arteriopalatinus of the pterygoid (usually a tiny groove, rather than a closed canal). To judge from the size of the bony foramen, this is a moderately large artery in *Batagur,Callagur, Kachuga, Morenia, Hardella, Orlitia* and *Siebenrockiella.* This artery has the position of the artery indicated by grooves on the parasphenoid of labyrinthodonts and there called the palatine artery,[1] and accordingly, I term it the palatine artery here, although in most Testudinidae it appears to be a vestigial, almost functionless structure. The artery of much larger size seen in sea turtles and called the arteria palatinonasalis by Nick (1913) appears to be homologous in that it is a forwardly directed branch of the carotid that is separated from the cerebral carotid by the trabecula cranii (represented in the adult by the lateral border of the pituitary fossa of the basisphenoid). There is usually an anastomotic artery between the Vidian and palatine arteries.

The carotid enters the foramen caroticum primitivum to pass into the pituitary fossa. Here there is a small anastomosis between the left and right arteries behind the pituitary (presumably, a circle of Willis), but the main artery (now the arteria carotis cerebralis) breaks up into branches in the meninges.

To generalize, apart from vestigial twigs, the separation between carotid and stapedial arteries in Testudinidae and *Chelydra* represents a segregation of blood for the brain (carotid) from blood for the rest of the head (stapedial artery). Furthermore, the stem of the supraorbital and infraorbital arteries is extracranial.

II. THE PATTERN OF THE KINOSTERNIDAE

Bony canals and foramina: — I have been able to examine skulls of *Kinosternon, Sternotherus, Claudius, Staurotypus,* and *Dermatemys.* The most conspicuous difference from the testudinid condition is the absence of the canalis stapediarterialis and foramen stapedio-temporale, or else the reduction of the canal to a very small pore. The foramen caroticum definitivum is relatively larger than that of testudinids, as is the canalis caroticus. The canalis caroticus leads forward to the level of the pituitary fossa and there divides into two openings: the outer and larger opening

[1] For a brief review of the position of the groove for the palatine (= palatal = nasopalatine) artery in labyrinthodonts see Romer (1947, pp. 44-45, fig. 8).

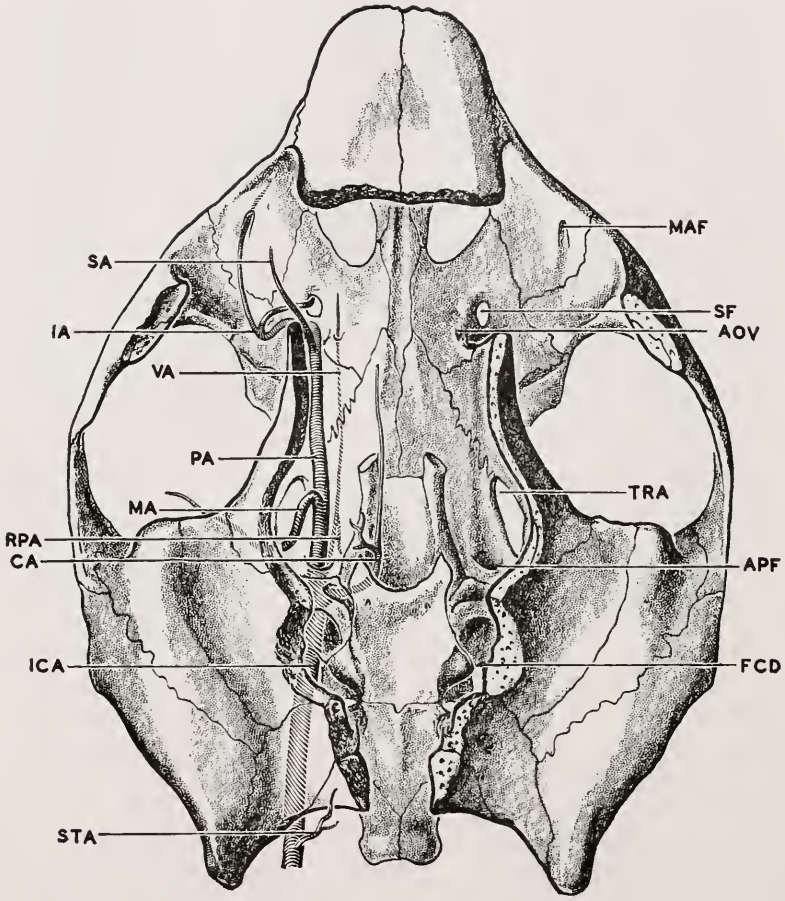

Figure 2. Dorsal view of arterial circulation (left side) and arterial foramina (right side): kinosternid pattern (semidiagrammatic), based on *Kinosternon sonoriense*. Abbreviations as in Figure 1; also, AOV, anterior opening of Vidian canal; FCD, foramen caroticum definitivum; RPA, recurrent pharyngeal branch of Vidian artery (a small artery supplying pharyngeal epithelium and passing through the pterygoid by the foramen carotico-pharyngeale); SF, suborbital foramen.

is that of the canalis arteriopalatinus, while the smaller, inner opening is the foramen caroticum primitivum. The opening of the canalis arteriopalatinus is ventral to the foramen cavernosum and is separated from that foramen by an horizontal lamina of the pterygoid. For convenience we may call this anterior opening of the canal the foramen arteriopalatinum, *new term.*

The Vidian canal is small and runs forward from an opening in the floor of the canalis arteriopalatinus. The Vidian canal is entirely buried in the pterygoid bone.

Arteries. I have dissected an injected *Sternotherus odoratus,* two uninjected *Kinosternon subrubrum,* and one uninjected *Kinosternon sonoriense.* The stapedial artery appears to be all but absent; in the *Sternotherus* and *K. sonoriense* a minute artery extended dorsally from the carotid stem behind the head and supplied the muscles at the rear of the temporal fossa; this probably represented the stapedial. In the *Kinosternon* specimens, branches of the vena capitis lateralis passed from the temporal fossa into a very small vestige of the foramen stapedio-temporale. Probably the occasional vestiges of this foramen seen in other Kinosternidae are similarly purely venous.

The carotid divides into a smaller arteria carotis cerebralis passing through the foramen caroticum primitivum and similar to that of testudinids, and a larger arteria palatina passing through the foramen arteriopalatinum. The blood for head structures other than the brain comes from the palatine artery. The palatine artery gives off a main (mandibular) branch that accompanies the mandibular nerve and supplies the jaw muscles, then, still within the cavum epiptericum, the palatine artery continues forward as a large vessel to the orbital region, where it breaks up into supraorbital and infraorbital branches distributed as in Testudinidae.

To generalize, in Kinosternidae nearly all the blood of the head passes through the canalis caroticus, and it is not until the single main head artery reaches the trabecula cranii and foramen caroticum primitivum that there is a segregation of blood for the brain from blood for the remainder of the head. This segregation takes place not behind the skull, as in Testudinidae, but within the cavum epiptericum. Further, the stem of the infraorbital and supraorbital arteries is intracranial.

III. DISCUSSION

In terms of the bony canals for arteries, the Testudinoidea (sense of Romer 1956) fall into two groups. One group contains *Chelydra, Macroclemys,* and the Testudinidae of Romer (1956). The other group contains *Dermatemys,* the Staurotypinae, and the Kinosterninae of Romer (1956). In testudinids there is a large foramen stapedio-temporale, but the foramen arterio-palatinum is small or minute. In the kinosternines the foramen stapedio-temporale is minute or absent, while the foramen arterio-palatinum is very large and conspicuous.

It would seem, since blood for the head other than the brain must come through one or the other of these foramina (except in land tortoises and some geoemydides,[1] where the mandibular branch of the stapedial is large), that reduction of the one foramen must lead to increase in the other. However, it does not seem likely that the testudinid condition is derived from the kinosternine pattern, for a large foramen stapedio-temporale, and, by inference, a well-developed temporal branch of the stapedial artery, is found in all turtles except the *Dermatemys*-Kinosterninae-Staurotypinae series, even in the Amphichelydia; moreover, this, the testudinid, type of stapedial artery is the type seen in Squamata, Rhynchocephalia, and Crocodilia.

On the other hand, the reduction of the palatine artery and consequent reduction of the foramen arteriopalatinum seen in Testudinidae and Chelydrinae is also a departure from the condition in other turtles and indicates a specialization in the opposite direction from that of kinosternines. Even in *Morenia, Orlitia,* and *Batagur,* where the foramen arteriopalatinum is the largest to occur in testudinids, the foramen is decidedly smaller than the foramen caroticum primitivum. Both arterial types might be derived from a pattern such as that of sea turtles (see Nick 1913 and Shindo 1914), where there is both a strong stapedial artery, primarily supplying the jaw musculature, and a strong palatine artery, primarily supplying the nasal and palatal region. The kinosternine pattern may be derived from this, probably primitive, pattern, by capture of the temporal circulation by the palatine artery, while the testudinid pattern may be derived by capture of the nasal and palatal circulation by the stapedial artery.

[1] I use the ending "-ide" for a suprageneric taxon to which I cannot yet assign with confidence a place in the taxonomic hierarchy.

Within each of the two groups of Testudinoidea, as defined by head arterial foramen pattern, there is relatively little variation. The most notable is that seen in *Gopherus* and some species of *Geochelone* (e.g., *G. pardalis* and *G. denticulata*, but not *G. gigantea* and *G. radiata*). Here, the lower (mandibular) ramus of the stapedial artery does not accompany the vena capitis lateralis anteriorly, but makes exit to the temporal fossa through its own foramen, here called foramen arteriomandibularis, *new term*, lying lateral to the foramen cavernosum. Other than this, the land tortoises are very similar to pond turtles, and their classification together in one family, Testudinidae, seems thoroughly warranted. (A foramen arteriomandibularis occurs as a variation in *Rhinoclemmys* and is always potential where the ramus mandibularis is large.)

The present findings do not, however, support the classification of Williams (1950) or its expanded form given in Romer (1956) in all details. This classification placed *Dermatemys* in a separate family (along with certain poorly known fossil genera), the Dermatemydidae; *Chelydra* and *Macroclemys* (syn. *Macrochelys*) formed the Chelydrinae, *Claudius* and *Staurotypus* the Staurotypinae, and *Kinosternon* and *Sternotherus* the Kinosterninae of a family Chelydridae;[1] *Platysternon* formed the Platysterninae, the pond turtles the Emydinae, and the land tortoises the Testudininae of a family Testudinidae. While the foramina for arteries in the main conform to this classification, particularly on such points as the close relationship between *Platysternon*, the pond turtles, and the land tortoises, and the close relationship between the Kinosterninae and the Staurotypinae, the arterial foramina suggest that *Dermatemys* is much more closely related to the Staurotypinae than is indicated by Williams' classification, and that *Chelydra* and *Macroclemys* are more closely related to the Testudinidae than to the remainder of Williams' Chelydridae. As here interpreted, *Chelydra* and *Macroclemys* are already committed to the testudinid evolutionary line in the reduction of the palatal artery (much more reduced than in many Old World emydines), while *Dermatemys* is committed to the kinosternid evolutionary line in its loss of the stapedial artery as indicated by the absence of a foramen stapedio-temporale.

Dermatemys, Staurotypus, and *Claudius* were grouped together by Boulenger (1889) in the Dermatemydidae. While later

[1]This association of kinosternines, staurotypines, and chelydrines in one family appears to date from Gray 1870.

work has demonstrated Boulenger's error in separating *Staurotypus* and *Claudius* from the kinosternines, the affinity between *Dermatemys* and the Staurotypinae suggested by Boulenger seems much more real to me than does the suggested affinity of the staurotypines and kinosternines with *Chelydra* and *Macroclemys*.

Several other points suggest that kinosternines are close to *Dermatemys,* while *Chelydra* and *Macroclemys* are close to the Testudinidae. Thus the kinosternines and *Dermatemys* have a conical and radially symmetrical footplate of the columella auris, while the footplate in chelydrines is flattened and disc-like, with the shaft arising from below the center; most testudinids have a columella as in chelydrines, but some Asiatic forms (e.g. *Morenia, Batagur, Orlitia*) approach kinosternines in the conical form of the footplate, although the asymmetry is marked.

Again, in kinosternines and *Dermatemys* there is a tight suture between basioccipital and opisthotic behind the acoustic papilla of the inner ear; *Chelydra* and *Macroclemys* agree with Testudinidae in the presence of an open fissure in the suture behind the apex of the papilla. Further, cloacal bursae are absent in *Dermatemys* and kinosternines, but present in *Chelydra* and *Macroclemys;* most aquatic Testudinidae have bursae (Smith and James).

The genus *Baptemys*, of the North American Eocene, appears to be intermediate morphologically between *Dermatemys* and the kinosternines. The genus is known from a number of shells, a few fragments of the limb skeleton, and two partial skulls. Of the skulls, one (in the Yale University Peabody Museum) is nearly complete. I have examined this skull and find it quite as figured by Hay (1908, pl. 37).

Baptemys agrees with both *Dermatemys* and the kinosternines in the absence of the foramen stapedio-temporale, the great forward extent of the posterior temporal emargination, and the entrance of the squamosal (quadrato-jugal Auct.) into the border of the posterior temporal emargination so that the postorbital is broadly excluded from the supratemporal (squamosal Auct.). *Baptemys* agrees with *Dermatemys* and differs from the kinosternines in: 1) having a moderately deep inferior temporal emargination; 2) having the trochlear process of the crista praetemporalis concealed from lateral view by the temporal arch; 3) having rather large frontals, with the interfrontal suture longer than the interprefrontal suture. *Baptemys* agrees with

kinosternines and differs from *Dermatemys* in: 1) absence of keels on the triturating surfaces; 2) high, acute coronoid process of the lower jaw; 3) lack of serrations on the jaw margins; and 4) reduction of the plastron. In one feature, *Baptemys* differs from both *Dermatemys* and the kinosternines: there is a complete series of neurals, separating the pleurals on the midline throughout the carapace.

It should be noted that the genera among the testudinid group that come nearest to the *Dermatemys*-kinosternine series are not *Chelydra* and *Macroclemys*, but the Asiatic *Batagur-Morenia*-series, where the foramen arteriopalatinum is less reduced than in other Testudinidae and the footplate of the columella auris is conical. The general appearance of the skull of *Dermatemys* is strongly reminiscent of *Batagur* and *Hardella*, particularly in such features as upturned nares, broad and complexly ridged triturating surfaces and broad muscular tuberosities of the basioccipital. This resemblance extends to the pes, for *Dermatemys* agrees with *Hardella*, *Kachuga*, *Callagur*, and *Batagur* in having four phalanges in the fifth toe (usually there are three or two phalanges in this toe in Testudinoidea).

Thus Asiatic "batagurs," on the one hand, and the Central American *Dermatemys*, on the other, appear to be near the base of the divergence of the testudinid and kinosternid series.

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TWO JURASSIC TURTLE SKULLS: A MORPHOLOGICAL STUDY

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WITH SIX PLATES

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No. 3 — *Two Jurassic Turtle Skulls: A Morphological Study*

By Thomas S. Parsons and Ernest E. Williams

Introduction

We here describe the detailed morphology of the skulls of two Jurassic turtles, one from the Portland Limestone of England, represented by three partial crania and one mandible (R2914, R3163, and R3164, British Museum, Natural History), and another from the Solenhofen of Bavaria, a cranium and mandible (4023) belonging to the Teyler Museum, Haarlem, Holland.

We deal with these specimens as examples of the morphology of turtle skulls in the Upper Jurassic. We do not attempt to assign them names or to place them taxonomically. The British Museum specimens have some similarity to *Stegochelys planiceps* (Owen) which is also from the Portland Limestone. This may well be what the Portland specimens should be called, but *Stegochelys planiceps* (Owen) is a genus and species founded upon a unique skull, and this type specimen is not at present to be found; the available figures (Owen, 1849-1884, plate 8) are somewhat idealized and do not compare in detail with the specimens at hand.

In the case of the Solenhofen skull we do not have any hint as to its proper name. It is surely a very different genus from the Portland one, exhibiting a remarkable combination of very specialized and primitive characters in contrast to the mostly primitive features of the Portland species. It is very probably a member of a different family from that to which the Portland form will be found to belong.

We might very safely provide a new generic and specific name for the Solenhofen skull, or with still greater security refer the Portland specimens provisionally to *Stegochelys planiceps*. We see, however, no great advantage in so doing. At present the higher taxonomy of Jurassic turtles is based exclusively upon shells. It would be necessary to have shells associated with these skulls in order to place them as to family. To devise or to use skull genera for these forms, when these skull genera will most probably in the not distant future be sunk in the synonymy of shell genera, would, we believe, serve no useful purpose.

Even at the familial level, exact assignment is impossible. We would suggest the following: they are surely amphichelydians and presumably pleurosternoids. Of the three families at present recognized in the Upper Jurassic of Europe, the Pleurosternidae, Plesiochelyidae, and Thalassemydidae, the first family is the most primitive, while the latter two are rather highly specialized and closely related; it would therefore be plausible to suppose that the Portland form is a pleurosternid and the

Solenhofen form either a plesiochelyid or a thalassemydid. This is, however, no more than a guess that the more primitive skull will be associated with the more primitive shell and the more specialized skull with the more specialized shell.

It should be pointed out that excellent *associated* skull and shell material of Jurassic age does exist in European collections. They are, however, at the moment almost unprepared and convey an absolute minimum of information. The skulls we here describe were all, when first seen, embedded in limestone to such an extent that only a turtle skull or mandible was apparent. Now, after preparation by acetic acid, even small cranial foramina may be probed with bristles and only the erosion of certain parts before fossilization prevents the description of these specimens from being as complete as that of any Recent skull. Many untouched skulls in pure limestones of Jurassic age would yield quite as well to similar techniques. Substantial advances in our knowledge await only the utilization of present opportunities.

Morphology

A detailed study of the structure of these specimens is presented in the following pages. We have found it convenient in places to contrast the Portland and Solenhofen materials by the device of parallel columns. In all such cases *the Portland specimens are discussed on the left and the Solenhofen on the right.*

The Skull as a Whole

In none of the available specimens is the skull roof well preserved. Posterolaterally, it is partially or completely lost, and the remainder is often somewhat cracked, thus making a detailed description of the general shape impossible. The dorsal surfaces of the roofing bones are rather rugose, though without well-defined sculpture, in the Portland skulls; they are quite smooth in the Solenhofen skull. However, in neither case can the sutures be found with any degree of certainty. In both forms, the skull is moderately high in lateral view and triangular when seen dorsally. The Solenhofen skull is somewhat lower and wider.

PORTLAND SPECIMENS

The roof of the *fossa temporalis* is mostly lost in the specimens, but was probably fairly complete. At least there is no indication of any marked emargination; however, the posterior and ventrolateral margins are not present. The orbits are quite large and face nearly directly laterally. Since their margins are incomplete, the shape cannot be described.

Most of the dorsal surface of the skull is nearly horizontal, sloping only slightly anteriorly. However, there is a very distinct angle in the region of the posterior end of the nasals and the anterior portion of the face faces anterodorsally, lying at approximately a forty-five degree angle to the horizontal. Thus the single median *apertura narium externa* faces anterodorsally. When seen in dorsal or ventral view, the part of the skull anterior to the orbits forms an equilateral triangle.

The primary palate possesses rather narrow, but much roughened triturating surfaces which are separated by a deep median trough into which the *aperturae narium internae* open. Each pterygoid possesses a well developed *processus pterygoideus externus;* thus the *fenestra subtemporalis* is comparatively small and posteriorly located. The *processus articularis* of the quadrate is well developed, and projects well ventral to the surface of the palate. It lies anterior to the level of the *condylus occipitalis.*

SOLENHOFEN SPECIMEN

The roof of the *fossa temporalis* is at least moderately complete. It is lost posteromedially and ventrolaterally, and was probably somewhat emarginate in the latter area; the posterior margin of the maxilla does not appear to be broken. The circular orbits are of moderate size and face dorsolaterally.

Most of the dorsal surface of the skull slopes anteriorly, at an angle of approximately thirty degrees, and there is no sharp angle when the skull is seen in lateral view. Thus the single median *apertura narium externa* faces more dorsally than anteriorly. The anterolateral surface of the skull is quite concave when seen in dorsal or ventral view; the snout, therefore, appears to be rather long and narrow.

There is a rather extensive and flat secondary palate formed largely by the maxillae, but also entered by the palatines. The posterior end of this palatal surface is notched, and forms the anterior margin of an oval median trough into which a single *apertura narium interna* opens. There is almost no trace of a *processus pterygoideus externus* on the pterygoid. Thus the *fenestra subtemporalis* is very large, reaching from the posterior margin of the maxilla to the *processus articularis* of the quadrate. The latter process is very short so that the wide *condylus mandibularis* is at essentially the same level as most of the palate; it projects somewhat posteriorly so that the mandibular and occipital condyles all lie in a straight transverse line.

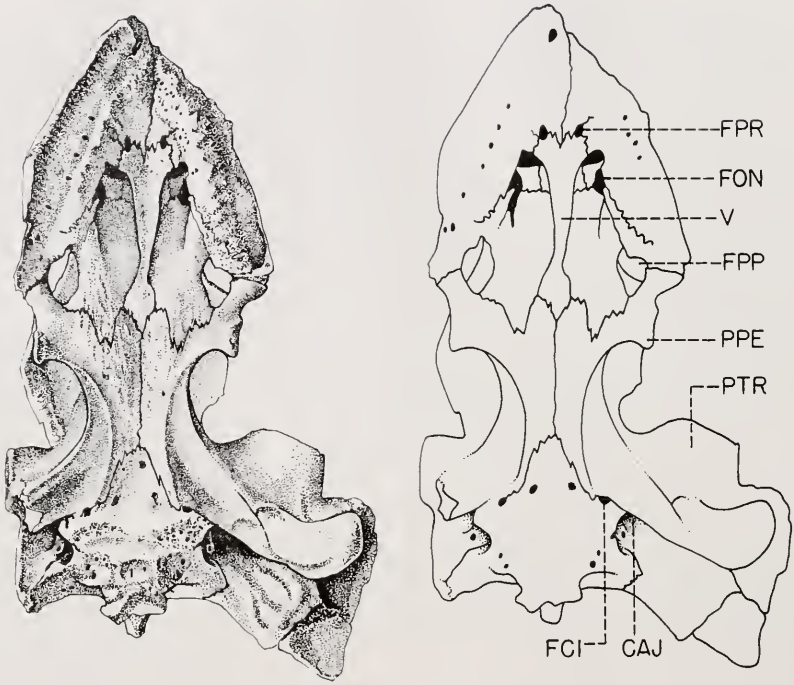

Fig. 1. Portland skull, British Museum R2914. Palatal view. Abbreviations: CAJ, cavum acustico-jugulare. FCI, foramen posterior canalis carotici interni. FON, foramen orbito-nasale. FPP, foramen palatinum posterius. FPR, foramen praepalatinum. PPE, processus pterygoideus externus. PTR, processus trochlearis. V, vomer.

Posteriorly, in each the *cavum tympani* is well developed, and much like that of recent turtles. It is connected to the large *fenestra postotica* by an *incisura columellae auris*. The massive paroccipital extension of the otic capsule characteristic of turtles is also like that of recent forms. The *crista supraoccipitalis* is broken off so that its extent and shape cannot be determined.

Skull Roof

Os parietale

The parietals roof over the median portion of the posterior half of the skull. Anterodorsally, they meet the frontals in a transverse suture near the midline, and, farther laterally, are in contact with the postorbitals. Their posterior and posterolateral portions are either missing

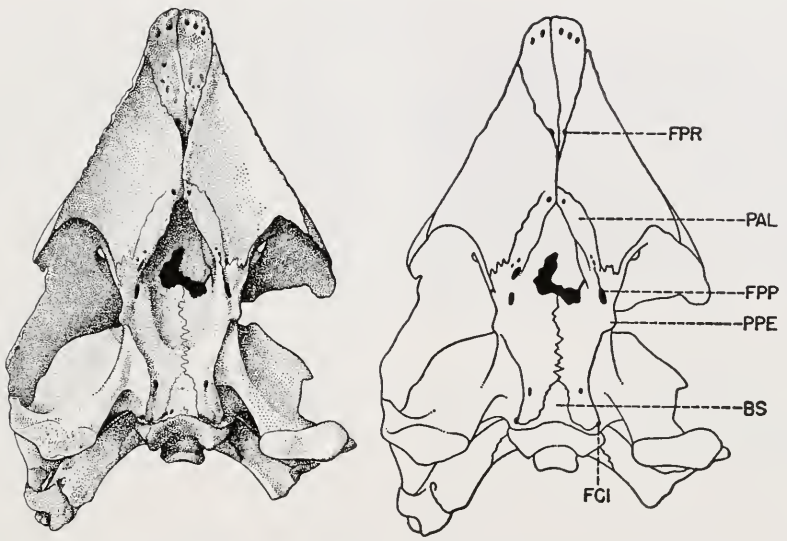

Fig. 2. Solenhofen skull, Teyler Museum. Palatal view. Abbreviations: BS, basisphenoid. FCI, foramen posterior canalis carotici interni. FPP, foramen palatinum posterius. FPR, foramen praepalatinum. PAL, palatine. PPE, processus pterygoideus externus.

or have no visible sutures. In neither form is there any extensive posterior emargination of the parietals; whether or not a small one was present cannot be determined. Paramedially the parietal sends down a vertical *processus inferior parietalis* which meets the supraoccipital posteriorly, the proötic, and the epipterygoid anteriorly. This process forms the dorsal wall of the large *foramen nervi trigemini.*

PORTLAND SPECIMENS

The parietal is in contact with the *crista pterygoidea* only at the anterior and posterior margins of the *foramen nervi trigemini*; anteriorly the parietal and the pterygoid are separated by the large epipterygoid.

SOLENHOFEN SPECIMEN

The parietal is completely separated from the pterygoid by the well-developed epipterygoid anteriorly and by the proötic posteriorly.

Os frontale

PORTLAND SPECIMENS

The frontal appears (the sutures are very obscure) to be a small trapezoidal element when seen in dorsal view. It is bounded posteriorly by the parietal, medially by the other frontal, anterolaterally by the prefrontal, and laterally by the postorbital. It does not, if this interpretation is correct, enter the margin of the orbit.

SOLENHOFEN SPECIMEN

The sutures are very indistinct, and the shape of the frontal as seen dorsally cannot be described with certainty. It appears to be bounded by the parietal posteriorly, by the other frontal medially, and by the postorbital posterolaterally. It probably does enter the margin of orbit. Anteriorly the bone is too eroded for any sutures to be visible.

Each frontal possesses a small parasagittal ridge along its ventral surface; between these ridges is a narrow *suleus olfactorius* which is widely open ventrally.

Os praefrontale

The prefrontal consists of a horizontal plate on the dorsal surface of the skull and a large, more or less vertical plate extending ventrally to meet the bones of the palate. The latter plate forms the bony septum between the orbit and the *fossa nasalis*.

PORTLAND SPECIMENS

In dorsal view the prefrontal is a rather irregularly shaped bone, the boundaries of which are not always clear. The horizontal plate is very thick. Medially it is bounded by the other prefrontal, posteromedially by the frontal, posterolaterally by the postorbital, laterally by the orbit, anterolaterally by the maxilla, and anteromedially by the nasal. These sutures appear to be essentially straight except for that with the maxilla which runs posteriorly from the nasal-prefrontal suture and then turns abruptly anterolaterally to run to the anterior end of the orbit. From there it extends ventrally between the vertical plate of the prefrontal and the maxilla.

SOLENHOFEN SPECIMEN

Due to the erosion of the anterodorsal part of the skull roof, the shape of the horizontal plate of the prefrontal cannot be determined.

Along the ventral surface of the prefrontal the *sulcus olfactorius* continues anteriorly from the frontal.

The vertical plate forms a broad, roughly transverse sheet of bone, the ventral end of which curves posteriorly, especially in its medial half. Laterally, the entire length of the plate possesses a suture with the vertical portion of the maxilla; medially, it forms the dorsal three-quarters of the margin of the *fissura ethmoidalis*. This fissure, which is roofed by the horizontal plates of the prefrontals, is quite wide dorsally and becomes gradually narrower ventrally. The posteroventral margin of the vertical plate is somewhat notched by the anterior margin of the *foramen orbito-nasale*.

PORTLAND SPECIMENS

Medial to this foramen, the prefrontal is broadly joined with a small dorsal process on the vomer anteromedially and, farther posterolaterally, with the anteromedial margin of the palatine. The *foramen orbito-nasale* is large and circular.

SOLENHOFEN SPECIMEN

Medial to this foramen, the prefrontal forms a suture with a small dorsal process on the vomer. It probably also joined the palatine as in the Portland skulls; however the anterior portion of the palatine is broken in the specimen so that there is now no contact, and the shape of the *foramen orbito-nasale* cannot be determined.

Os nasale

PORTLAND SPECIMENS

The nasals are small, roughly rectangular elements forming the roof of the *fossa nasalis*. Anteriorly, they form the essentially transverse dorsal border of the *apertura narium externa*. Their sutures are not clear, but each appears to possess a straight parasagittal connection with the maxilla laterally, a sagittal suture with the other nasal medially, and a roughly transverse one with the prefrontal posteriorly. The nasals are thickest posteriorly, and taper to a thin edge anteriorly.

SOLENHOFEN SPECIMEN

The nasals are not known; due to the erosion of this portion of the skull it cannot even be seen whether or not they were present.

Os postorbitale

The postorbital is not well preserved in either form. Parts of it are missing, and the sutures are very indistinct. Thus its posterior and ventral portions cannot be described.

PORTLAND SPECIMENS

The postorbital probably possessed an anteromedial suture with the prefrontal (thus excluding the frontal from the margin of the orbit), a medial suture with the frontal, and a posteromedial one with the parietal.

SOLENHOFEN SPECIMEN

The postorbital was probably smaller than in the Portland form, and was bounded anteriorly by the frontal (which thus enters the margin of the orbit).

Os jugale

PORTLAND SPECIMENS

The jugal is not well known since this area is almost completely lost. Part of it is preserved in R3164, and appears to lie between the maxilla and the postorbital at the posteroventral corner of the orbit.

SOLENHOFEN SPECIMEN

The sutures are difficult to see, but the jugal is apparently a rather small element, although its posterior edge is probably broken so that its full extent is uncertain. This bone forms the posteroventral wall of the orbit, having a vertical portion which extends ventrally from the postorbital to the maxilla; it is triangular in section. The jugal apparently lies dorsal to the maxilla, and does not reach the outer margin of the triturating surface or the palate (the suture with the maxilla cannot be seen on the outer side of the cheek). A fairly short but stout process runs posteromedially from the vertical portion, bounded ventrally by the maxilla and medially by the palatine. The end of this process lies on the dorsal surface of the *processus pterygoideus externus* of the pterygoid. A small foramen enters the suture between the jugal and the palatine near the posterior

SOLENHOFEN SPECIMEN

end of this process, and two other foramina are present well ventrally on the posterior face of the vertical portion of the jugal.

Os quadrato-jugale

The quadrato-jugal is not known; this area is mostly lost, and badly broken and eroded where present.

Os squamosum

PORTLAND SPECIMENS

The squamosal is not known with certainty, but is probably represented by two fragments of bone, one posterior and one posterodorsal to the margin of the *cavum tympani* of the quadrate. The more posterior of the fragments is in contact with the extreme lateral end of the opisthotic posteroventrally. There is a small hole between the posterodorsal part of the *cavum tympani* and the posterior end of the more dorsal of the two fragments; presumably this represents the remains of an *antrum postoticum*.

SOLENHOFEN SPECIMEN

The squamosal forms a small cap of bone lying above and behind the posterodorsal third of the margin of the *cavum tympani* of the quadrate. Anterolaterally, it is continuous with another (unidentifiable) bone of the skull roof. Its ventral margin lies on the quadrate except at the extreme posteromedial corner where it meets the opisthotic on the floor of the *fossa temporalis*. The posterior extremity of the squamosal is missing in this specimen. The bone is everywhere thin and contains a moderately large *antrum postoticum* which is widely open into the *cavum tympani*.

Palatal Elements

Os praemaxillare

The premaxilla is a small, roughly triangular element which is narrowest posteriorly. Medially, it is bounded by the other premaxilla and posterolaterally by the maxilla.

PORTLAND SPECIMENS

The anteriormost end is missing so that it is impossible to know whether the tip of the upper jaw was hooked, notched, or plane.

Both the tomial ridge and the

SOLENHOFEN SPECIMEN

The anterior margin of the premaxilla is rather gently curved when seen in ventral view and it is neither hooked nor notched.

Lingual ridges are not present,

PORTLAND SPECIMENS

lingual ridge are large; between them there is a deep channel on the palatal surface. The ridges and channel are continuous with those of the maxilla. There is, in the midline, a narrow groove separating the lingual ridges of opposite sides. Posteriorly, the palatal surface of the premaxilla ends in a short transverse suture with the vomer. This suture is well dorsal to the level of the lingual ridges. Lateral and anterolateral to the vomeral suture, the premaxilla forms the anterior margin of the nearly circular *foramen praepalatinum*. At the anterolateral corner of this foramen, the premaxilla just barely touches the vomer again, thus excluding the maxilla from the margin of the foramen ventrally.

SOLENHOFEN SPECIMEN

and the palatal surface is quite smooth, although it forms a sharp tomial margin. The two premaxillae appear as a long wedge, bounded for their entire posterolateral margin by the maxilla; the vomer does not appear on the palate. Just inside the tomial margin on the palatal surface of each premaxilla, there are three prominent nutritive foramina. Near the posterior end of the maxillary-premaxillary suture there is, on either side, a very small foramen leading to the *fossa nasalis*. They are not symmetrical and could be the result of weathering of the skull, but are more probably very small vestiges of the *foramina praepalatina*. On one side, the foramen appears to be completely surrounded by the premaxilla, and, on the other, the maxilla enters its margin.

Dorsally, the premaxillae form the ventral margin of the single *apertura narium externa* which is essentially transverse with the lateral corners slightly rounded. There is no indication of any bony separation of the two *nares externi*. Running along the midline between the anterior facial surface of the premaxilla and its suture with the vomer dorsally, there is a markedly thickened and raised portion of the bones; lateral to this, each is much lower and thinner. At the anterior end, this ridge is divided by a median (nutritive?) foramen entering the bone of the snout.

PORTLAND SPECIMENS

To each side of the median ridge there is a marked groove running from the *foramen praepalatinum* to a large anterior foramen which continues anteriorly into the thick anterior face of the premaxilla. Besides forming the anterior and

SOLENHOFEN SPECIMEN

The median ridge widens anteriorly where it surrounds the median foramen and overlies a small groove. This groove appears to lead into a canal running anteriorly within the premaxilla. The vomer meets the premaxilla only at the

PORTLAND SPECIMENS

medial margins of the *foramen praepalatinum*, the premaxilla sends a very narrow process along its lateral margin to meet the vomer posteriorly and thus exclude the maxilla from the margin of the foramen.

SOLENHOFEN SPECIMEN

top of the ridge; laterally the maxilla and premaxilla are in contact. The *foramina praepalatina* appear essentially the same as they do in a palatal view.

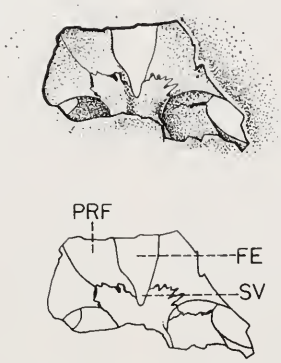

Fig. 3. Portland skull, British Museum R2914. Bones within apertura narium externa (edge broken) as seen in anterior view. Abbreviations: FE, fissura ethmoidalis. PRF, prefrontal. SV, sulcus vomeri.

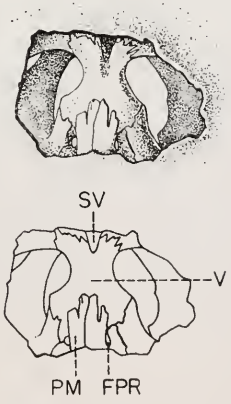

Fig. 4. Portland skull, British Museum R2914. Bones within apertura narium externa (edge broken) as seen in anterodorsal view. Abbreviations: FPR, foramen praepalatinum. PM, premaxilla. SV, sulcus vomeri. V, vomer.

Os maxillare

The maxilla is a large element with two main portions, a vertical part and a horizontal part. The former forms the surface of the face anterior and ventral to the orbit. Anteroventrally, it is bounded by the premaxilla and, posterodorsal to the latter, it forms the lateral margin of the *apertura narium externa.*

PORTLAND SPECIMENS

Posterodorsal to the narial opening it is bounded medially by the nasals and finally, at its dorsalmost end, by the prefrontal. The suture with the prefrontal continues ventrally along the anterior margin of the orbit. The maxilla continues posteriorly as a rather narrow wall ventral to the large orbit. The posterior portion is incompletely preserved, but appears to be bounded posterodorsally by the remains of the jugal. The lateral surface of the vertical plate of the maxilla possesses only a very few nutritive foramina.

SOLENHOFEN SPECIMEN

The dorsal extension of the maxilla between the narial opening and the orbit is eroded and the sutures cannot be seen. At the anteroventral corner of the orbit, it possesses a suture with the prefrontal as in the Portland form. The maxilla continues posteriorly as a deep bar ventral to the rather small orbit. It has a suture with the jugal along the posteroventral margin of the orbit. Farther posteriorly, sutures cannot be seen. There are large numbers of nutritive foramina along the lateral surface of the maxilla.

Internally, the maxilla forms the lateral and ventrolateral walls of the *fossa nasalis.* At the posterolateral corner of the nasal fossa and at the lateral edge of the *foramen orbito-nasale*, lies the *foramen alveolare superius* which leads into the *canalis alveolaris superior*; the various nutritive foramina of the facial and palatal surfaces of the maxilla are all connected with this canal.

PORTLAND SPECIMENS

The maxilla forms the floor of the orbit laterally. Anteriorly it is in contact with the ventrolateral portion of the prefrontal and posteriorly with the *processus pterygoideus externus* of the pterygoid.

SOLENHOFEN SPECIMEN

The maxilla forms only a small part of the floor of the orbit anterolaterally. It is bounded anteriorly by the prefrontal, anteromedially by the margin of the *foramen orbito-nasale,* posteromedially by

PORTLAND SPECIMENS

Between these two, it forms a suture with the palatine. The maxillary suture with the palatine is separated from that with the prefrontal by the *foramen orbitonasale*, and its suture with the palatine separated from that with the pterygoid by the *foramen palatinum posterius*; the maxilla forms the lateral margin of both of these large foramina.

SOLENHOFEN SPECIMEN

the palatine, and posterolaterally by the jugal.

Posterior and lateral to the premaxilla, most of the palate is formed by the horizontal portion of the maxilla.

PORTLAND SPECIMENS

This is a rather long, narrow element with a very prominent tomial ridge and, along its medial edge, an equally prominent lingual ridge; between the two there is a deep channel. Both the ridges and the channel are continuous with those of the premaxilla. The tomial ridge is sharp but quite even, while the lingual ridge has an irregular, roughened surface. The *apertura narium interna* lies medial to the center of the maxilla which forms its anterolateral and lateral margins. Anterior to the apertura, the maxilla extends slightly medially and dorsally to meet the vomer. Anterior to the vomer it forms a suture with the premaxilla and is narrowly excluded from the margin

SOLENHOFEN SPECIMEN

This is a large plate since this form has a well-developed secondary palate. The tomial ridge is low but sharp, and the remainder of its surface is smooth. It is bounded anteromedially by the premaxilla, medially by the other maxilla, and posteromedially by the palatine which excludes it from the margin of the *apertura narium interna*. At its extreme posterior end it meets the reduced *processus pterygoideus externus* of the pterygoid. The concave posterolateral margin of the maxilla borders the *fenestra subtemporalis*. Numerous, moderate-sized nutritive foramina occur along the tomial ridge and scattered larger ones are present on the palatal surface. The former give

PORTLAND SPECIMENS

of the *foramen praepalatinum*. Posterior to the *apertura narium interna*, it joins the palatine anterior to the large oval *foramen palatinum posterius* and forms the lateral margin of that foramen. The *processus pterygoideus externus* of the pterygoid meets the maxilla at the posterior end of the deep channel between the tomial and lingual ridges. In the channel are a few moderately large nutritive foramina; there are fewer and smaller ones on the tomial ridge. The posterolateral corner of the maxilla is not preserved.

SOLENHOFEN SPECIMEN

the tomial ridge a somewhat serrate appearance.

Os palatinum

The palatine is a plate of bone forming the portion of the palate medial to the posterior half of the maxilla.

PORTLAND SPECIMENS

In palatal view the two palatines are separated by the vomer with which they are in contact throughout their entire length. Each forms a rather flat plate which is farthest dorsal at its anteromedial corner where it forms a short suture with the ventromedial portion of the prefrontal; from there it slopes posteroventrally. Posteriorly it possesses a rather irregular suture with the pterygoid. Laterally, it forms the medial margin of the *foramen palatinum posterius* and the posteromedial margin of the *foramen orbito-nasale*. Between these foramina a massive process extends ventrolaterally to meet the posteromedial edge of the maxilla where it forms a small posterior

SOLENHOFEN SPECIMEN

Due to the formation of a secondary palate, each palatine forms a much folded plate which is, anteriorly, C-shaped in transverse section. It possesses a rather small, lenticular, horizontal portion along the posteromedial margin of the secondary palate. This portion is bounded anterolaterally by the maxilla and posteromedially it forms the margin of the *apertura narium interna*. Anteriorly the two palatines are in contact to exclude the maxilla from the margin of the *apertura*. Posteriorly the palatal surface of the palatine possesses a short suture with the pterygoid. The palatine continues dorsally from its line of suture with the maxilla and then arches dorsomedially to meet the

PORTLAND SPECIMENS

portion of the prominent lingual ridge. The medial half of the palatine forms the roof of the *apertura narium interna*. The vomer extends somewhat ventral to the medial portion of the palatine so that there is a distinct groove between the vomer and the lateral portion of the palatine.

The dorsal surface of the palatine forms most of the floor of the orbit; its relations there are the same as on the ventral surface except that the two palatines meet in a sagittal suture dorsal to the vomer for the posterior two-thirds or three-quarters of their length.

SOLENHOFEN SPECIMEN

other palatine in a sagittal suture along the roof of a deep, median trough. Thus the *apertura narium interna* is surrounded by the palatines. The vertical and dorsal parts of the palatine continue a short distance posterior to the maxilla and are there bounded laterally by the pterygoid. On the left side there is a small oval *foramen palatinum posterius* between the palatine and the pterygoid; on the right it is divided into two foramina, a more posterior oval one like that on the left and a smaller circular one completely within the palatine just anterior to the first. There are one or two small foramina near the posterior end of the secondary palatal surface of the palatine. Posteriorly the palatine was almost certainly in contact with the pterygoid, but on the specimen the posterodorsal portion of the former is missing.

The dorsal surface of the palatine forms the ventromedial wall of the orbit. Anteriorly the dorsal part is somewhat broken, but meets the vomer anteromedially. Lateral to that it almost certainly possessed a suture with the ventromedial edge of the prefrontal and formed the posteromedial margin of the *foramen orbito-nasale*.

Vomer

PORTLAND SPECIMENS

The vomer extends from the premaxillae to the pterygoids, forming a long narrow bar along the center

SOLENHOFEN SPECIMEN

The vomer is much reduced and does not appear on the palate at all, but forms a short, rather stout

PORTLAND SPECIMENS

of the palate. Anteriorly it is a rather stout element which has a short transverse suture with the premaxilla and which forms the posterior and, on the ventral surface, much of the medial and lateral margins of the nearly circular *foramen praepalatinum*. Anterolaterally a short, broad process extends ventrolaterally to meet the medial surface of the palatal exposure of the maxilla. Posterior to this process it forms the anteromedial and medial margins of the *apertura narium interna* and continues posteriorly as a narrow rod between the palatines to meet the pterygoids. This posterior portion extends slightly ventral to the palatines which meet in the midline dorsal to the vomer. The ridge thus formed is highest anteriorly and disappears posteriorly where the vomer and palatines form an essentially even surface. For the anterior three-quarters of its length, the vomer slowly narrows posteriorly; the posterior quarter is again wider, though not as wide as the anterior end.

SOLENHOFEN SPECIMEN

vertical element lying dorsal to the sagittal suture between the maxillae and palatines on the secondary palate. Thus the vomer separates the anterior halves of the two *meati choanarum* which lead from the *fossa nasalis* to the *aperturae narium internae*.

The vomer possesses, on its dorsal surface, a pair of short, rather stout processes; they are very near its anterior end in the Portland skulls, but occupy most of the length of the greatly reduced vomer of the Solenhofen form. Each process meets the vertical plate of the prefrontal dorsally and the anteromedial edge of the palatine posterolaterally. The latter contact is missing in the Solenhofen skull due to breakage of the palatines; however, it was almost certainly present. Between the two dorsal processes of the vomer there is a narrow groove, the *sulcus vomeri*. The sulcus forms the ventral quarter of the *fissura ethmoidalis*.

Os pterygoideum

The pterygoids are paired, more or less crescentic elements which form most of the posterior half of the palatal surface of the skull. They meet in a sagittal suture for much of their length and, on their ventral surface, widely separate the palatines from the basisphenoid.

PORTLAND SPECIMENS

Anteromedially the pterygoid is bounded by the palatine and lateral to this it forms the posterolateral margin of the large *foramen palatinum posterius*. Anterolaterally there is a massive *processus pterygoideus externus* which has a thin anterior portion along the posterior palatine foramen and meets the posterior end of the maxilla. The major part of the process is laterally directed and its end is slightly expanded dorsally and ventrally, much as in *Chelydra*. Thus the lateral margin of the pterygoid is markedly concave anteriorly, and there is a fairly marked waist to the united pterygoids.

SOLENHOFEN SPECIMEN

The anterior part of the pterygoid is greatly arched, so that the deep median trough continues posteriorly from the palatines. There is almost no *processus pterygoideus externus*, although the pterygoid does possess a short transverse suture with the posteromedial end of the maxilla. The suture between the pterygoid and palatine runs a short distance posteriorly from the maxillary contact and then becomes transverse, extending to the midline. Due to breakage of the palatine, the medial portion of this suture is not present. The small oval *foramen palatinum posterius* lies in the parasagittal portion of the pterygoid-palatine suture. A small nubbin, which represents the remnant of a *processus pterygoideus externus*, extends ventrolaterally from the lateral margin of the pterygoid a short distance posterior to the *foramen palatinum posterius*. The lateral margin of the anterior half of the pterygoid thus is essentially straight and nearly parasagittal with its anterior ends only slightly more lateral than its center, and there is no waist to the united pterygoids.

Posteriorly the ventral surface of the pterygoid sends out a long wing, somewhat curved, which lies along the ventral surface of the *processus articularis* of the quadrate. This wing forms the posteromedial margin of the large *fenestra subtemporalis*. Medial to the wings, the two pterygoids are separated by the roughly triangular basisphenoid with which they have posteromedial sutures. There is a slight ridge on the ventral surface of the pterygoid which curves posteromedially and posteriorly from the posterior end of the *processus pterygoideus externus* to the posterior end of the pterygoid-basisphenoid suture; it presumably served for attachment of the pterygoid muscle.

Posteriorly, the pterygoid is in contact with the basioccipital. Just anterior to their suture and lateral to the small ridge, the small *foramen posterior canalis carotici interni* enters the pterygoid which completely surrounds it. Between the carotid foramen and the lateral margin, the pterygoid contains a large and deep posteroventral concavity. The floor of this concavity forms the ventral margin of the large *fenestra postotica*.

PORTLAND SPECIMENS

Along the medial portion of this margin, the pterygoid has a short suture with the anteroventral end of the exoccipital.

SOLENHOFEN SPECIMEN

The posterior margin of the pterygoid is here concave, and does not reach the anteroventral end of the exoccipital. There is a small foramen on the ventral surface of each pterygoid slightly anterior to the carotid foramen and medial to the small ridge.

In lateral view the pterygoid appears rather small. Posterodorsally it possesses a long suture with the quadrate, and more anteriorly a dorsal one with the large epipterygoid. The *crista pterygoidea* is very low anteriorly, but rises dorsally in the region of the *foramen nervi trigemini* where it is notched to form the ventral margin of the foramen.

PORTLAND SPECIMENS

The crista meets the parietal at either side of the foramen and is thus separated from the proötic by the parietal and quadrate.

SOLENHOFEN SPECIMEN

The crista is bounded posterodorsally by the proötic. Both the latter bone and the epipterygoid reach the margin of the foramen and thus separate completely the pterygoid and the parietal.

At the base of the *crista pterygoidea*, between the epipterygoid and quadrate, there is an irregular depression as if those two bones possessed an unossified connection lying lateral to the pterygoid.

The dorsal surface of the pterygoid is partly concealed in the specimens, but much of its structure may be seen. Posteriorly it forms much of the floor of the large *cavum acustico-jugulare*.

PORTLAND SPECIMENS

The proötic and the large *processus interfenestralis* of the opisthotic are sutured to the posterodorsal surface of the pterygoid.

SOLENHOFEN SPECIMEN

There is no bony connection between the opisthotic and the pterygoid. Presumably the proötic does meet the dorsal surface of the pterygoid, but the area cannot be seen clearly.

Most of the medial portion of the pterygoid is overlain by the basisphenoid; the large *rostrum basisphenoidale* reaches nearly, if not actually, to the anterior margin of the pterygoid. The other bones which articulate with the dorsal surface of the latter element are those described in the lateral view. There is a wide *sulcus cavernosus* along the dorsal surface of the pterygoid lateral to the basisphenoid and proötic and medial to the epipterygoid, *crista pterygoidea*, and quadrate. The various foramina are hard to see clearly, and the following description cannot be considered certain in all respects. The *canalis caroticus internus* at some point in its forward course leaves the pterygoid and enters the basisphenoid.

PORTLAND SPECIMENS

It is connected, about midway along its course, with the *sulcus cavernosus* by a small *foramen pro ramo nervi vidiani* which enters the sulcus between the pterygoid and the proötic.

Anteriorly the course of the vidian nerve cannot be determined with

SOLENHOFEN SPECIMEN

The carotid canal is connected in some fashion with the canal from the foramen which may transmit the vidian nerve. The latter opens to the dorsal surface of the pterygoid well anteriorly, just lateral to the *rostrum basisphenoidale*.

There is no separate *canalis nervi*

PORTLAND SPECIMENS

certainty. There appears to be a small foramen in the pterygoid just lateral to the *rostrum basisphenoidale* which may transmit it; the foramen could not be traced with a bristle. In one specimen (R3164) there is a small *canalis nervi vidiani* running between the pterygoid and epipterygoid from the region of the foramen mentioned above to the anterior end of the suture between these bones; there is no trace of it in another specimen (R2914), and the situation is not clear in the third (R3163). A pair of small (nutritive?) foramina occur on the ventral surface of the pterygoids, near the lateral margin in the region of greatest lateral constriction.

SOLENHOFEN SPECIMEN

vidiani between the pterygoid and the epipterygoid.

Os epipterygoideum

The epipterygoid is a fairly large plate rising dorsally from the pterygoid to meet the *processus inferior parietalis*. Its ventral margin is horizontal and smooth, but its dorsal suture is irregular. A thin posteroventral process extends towards, but does not quite reach, the quadrate.

PORTLAND SPECIMENS

The pterygoid and parietal send narrow processes to meet each other on the anterior margin of the *foramen nervi trigemini* and thus exclude the epipterygoid from the margin of this foramen. The *canalis nervi vidiani* runs between the anteroventral border of the epipterygoid and the pterygoid in at least one specimen (see the description of the pterygoid concerning the variation in this canal).

SOLENHOFEN SPECIMEN

The epipterygoid forms the anteroventral margin of the *foramen nervi trigemini*, thus separating the pterygoid from the parietal. Along the margin of the foramen, there is a pronounced lip which extends laterally and bears a blunt ventral process so that the slightly concave lateral surface of the bone has a marked groove anteroventral to the lip.

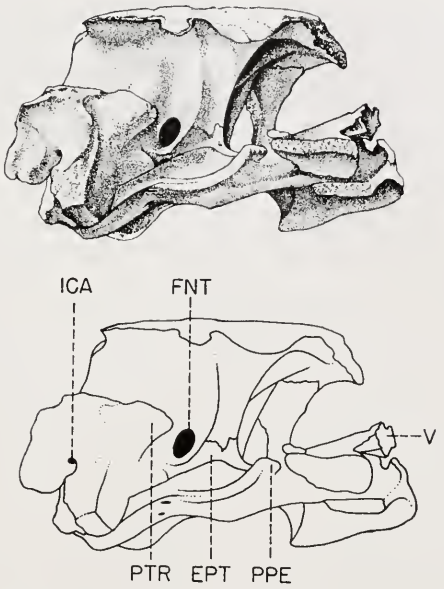

Fig. 5. Portland skull, British Museum R3164. Lateral view of skull fragment. Abbreviations: EPT, epipterygoid. FNT, foramen nervi trigemini. ICA, incisura columellae auris. PPE, processus pterygoideus externus. PTR, processus trochlearis. V, vomer.

Elements of the Braincase and Otic Region

Os basisphenoideum

The basisphenoid forms a small, roughly triangular element when seen in palatal view. It is bounded anterolaterally by the pterygoids and posteriorly by the basioccipital; the anterior apex of the triangle is rounded. A parasphenoid is not present as a distinct element, although it is possible that the remnants of one are fused with the basisphenoid.

PORTLAND SPECIMENS

The posterior end of the basisphenoid is very slightly concave, and raised into a low transverse ridge across the flat palatal surface of the skull.

SOLENHOFEN SPECIMEN

The posterior end of the basisphenoid is essentially transverse. It is not raised, but gives the impression of a ridge due to the marked difference in angle between the ventral surfaces of the basisphenoid and the basioccipital.

Dorsally, the basisphenoid is more extensive and forms a considerable part of the floor of the cranial cavity. Besides its lateral contact with the pterygoids, which it also overlies anteriorly, and its posterior suture with the basioccipital, the basisphenoid possesses an extensive dorsolateral suture with the proötic. The dorsal surface can conveniently be divided into two main portions separated by the *dorsum sellae*.

The more posterior portion forms a large trough which is slightly concave medially. Posterolaterally this surface forms part of the ventral margin of the large *hiatus acusticus* or opening between the *cavum cranii* and *cavum labyrinthicum*, thus separating the basioccipital from the proötic. Each side of this dorsal surface is pierced by a small foramen, the posterior opening of the *canalis nervi abducentis*. The anterior opening of this canal is into the medial side of the *sulcus cavernosus*.

PORTLAND SPECIMENS

Anterior to the proötic suture, the lateral margin of the basisphenoid continues anteriorly as the *processus clinoideus*. This process extends a short distance dorsolaterally as well as anteriorly, and ends bluntly. Between the clinoid processes of opposite sides, the basisphenoid slopes anteroventrally, the sloping region being the *dorsum sellae*.

SOLENHOFEN SPECIMEN

Anterior to the proötic suture, a prominent shelf on the basisphenoid projects forward well dorsal to the anterior portion of the bone. The anterior margin of this shelf shows a broad median extension flanked by two large concavities, and, at the lateral margins, by two small projections or *processus clinoidei*. The *dorsum sellae*, between the anterior and posterior parts of the basisphenoid, is thus an essentially vertical face which is concave anteriorly.

Laterally the basisphenoid enters the medial wall of the *sulcus cavernosus*, thus separating the pterygoid and proötic anteriorly; the sulci converge anteriorly as the basisphenoid narrows. The anterior opening of the *canalis nervi abducentis* lies in the wall of the sulcus well anteriorly and just dorsal to the pterygoid-basisphenoid suture.

Anteriorly the basisphenoid forms a narrow projection, the *rostrum basisphenoidale*, which lies on the dorsal surface of the pterygoids. This rostrum terminates rather abruptly near the anterior end of the pterygoid; quite possibly it was continued forward dorsal to the palatines as a cartilaginous process. In transverse section the rostrum is formed by a pair of oval bars of bone, one on either side with the long axis of the oval horizontal. Between the ovals ventrally there is a very thin sheet of bone. Thus there is a median groove in the dorsal surface of the rostrum; the

posterior portion of this groove is the *sella turcica*. Although the entire rostrum is more flattened in the Solenhofen skull than in the Portland ones, the basic pattern is identical. At the posterior end of the *sella turcica*, between the bases of the thicker lateral portions of the rostrum, lie the entrances of the arterial circulation of the head, the *foramen anterior canalis carotici interni*. The foramen is paired in the Portland skulls, but appears to form a single median opening in the Solenhofen skull. The *canalis caroticus internus* must enter the basisphenoid from the pterygoid; the position and nature of this entrance are unknown.

Os basioccipitale

The basioccipital is a rather small but massive element at the posteroventral end of the skull. It makes up the greater part of the *condylus occipitalis*, and forms all of the pit for the reception of a *ligamentum apicis dentis*. The condyle lacks any pronounced neck and protrudes but slightly.

PORTLAND SPECIMENS

The basioccipital is excluded from the ventral margin of the *foramen magnum* by the two exoccipitals which meet above it.

Ventrally the *tubercula basioccipitales* are only slightly developed, and the crescentic precondylar fossa between them is shallow. It does not extend anteriorly as far as the basisphenoid.

SOLENHOFEN SPECIMEN

The basioccipital enters the floor of the *foramen magnum*, narrowly separating the two exoccipitals.

The *tubercula basioccipitales* are large and prominent, as is the precondylar fossa which extends anteriorly to the posterior margin of the basisphenoid.

The basioccipital is bounded dorsally by the exoccipital and anteriorly by the pterygoids and the basisphenoid.

PORTLAND SPECIMENS

Laterally the pterygoid and exoccipital are in contact thus excluding the basioccipital from the margin of the *fenestra postotica* and the *cavum acustico-jugulare*. The exoccipital-basioccipital suture is straight.

SOLENHOFEN SPECIMEN

Laterally the basioccipital enters into the ventromedial margin of the *fenestra postotica* and *cavum acustico-jugulare* between its sutures with the pterygoid and the exoccipital. The latter suture is irregular.

Dorsally, the basioccipital forms the posteromedian part of the floor of the *cavum cranii*. There is a moderate-sized *crista dorsalis basioccipitalis* at its anterior end in the Portland form; this crista is much reduced in the Solenhofen skull.

PORTLAND SPECIMENS

Due to the dorsal fusion of the basioccipital with the exoccipitals, the extent of the former cannot be determined. In the largest skull (R2914) both these elements appear to be excluded from the margin of the *hiatus acusticus*; however, in the small specimen (R3164) both appear narrowly to enter its posteroventral margin.

SOLENHOFEN SPECIMEN

The basioccipital makes only a thin median band in the floor of the *cavum cranii*; most of it is overlain by the exoccipitals from which it is separated by a very irregular suture. Anteriorly, however, it is exposed laterally, and narrowly enters the ventral margin of the *hiatus acusticus*.

Os exoccipitale

Each exoccipital is a small element lying lateral to the *foramen magnum*. It is in two main parts, a dorsolateral and a ventromedial. The dorsal portion is a rather narrow bar of bone lying posterior and ventromedial to the opisthotic. Dorsomedially, it possesses a short suture with the supraoccipital and forms the dorsolateral margin of the *foramen magnum*, and ventrolaterally it lies along the dorsomedial margin of the *fenestra postotica*.

From near the center of this dorsal bar, a strong process extends ventromedially to the basioccipital. Medially this process forms the ventrolateral margin of the *foramen magnum*, and laterally it enters into the medial margin of the *fenestra postotica*.

PORTLAND SPECIMENS

The process expands laterally where it meets the pterygoid posterolaterally and possesses a long suture with the ventral margin of the opisthotic. Medially, the process forms the dorsolateral portion of the *condylus occipitalis*, and appears to meet the opposite exoccipital, thus excluding the basioccipital from the *foramen magnum*.

SOLENHOFEN SPECIMEN

The process is rather small, and does not reach the pterygoid. Medially, but not laterally, it possesses a very short suture with the ventral margin of the opisthotic. Medially, the process forms the dorsolateral portion of the *condylus occipitalis*. The basioccipital enters the *foramen magnum* and thus separates the two exoccipitals.

At approximately the level of the top of the occipital condyle, the ventromedial process of the exoccipital is pierced by two small *foramina nervi hypoglossi.* One (larger in the Solenhofen skull; they are of equal size in the Portland form) lies slightly posterodorsal to the other. Anterolateral to these foramina, the exoccipital forms part of the margin of the *fenestra postotica.*

PORTLAND SPECIMENS

The medial portion of this fenestra is separated from the lateral part by a ventral process of the opisthotic and forms a canal for the *vena cerebralis posterior* and the vagus and accessory nerves. Its posterior opening, the *foramen jugulare posterius,* is bounded dorsally, medially, and ventrally by the exoccipital, with the opisthotic forming the lateral wall. At its opening into the *cavum cranii,* the *foramen jugulare anterius,* it is surrounded by the same two bones, with the exoccipital forming its dorsal, posterior, and ventral margins. The canal thus formed runs somewhat dorsally as well as anteromedially, and forms the anterior border of the exoccipital. About two-thirds of the way anteromedially along the canal there is a prominent *fenestra perilymphatica*; this lies mainly within the opisthotic, but the exoccipital may form part of its ventral margin. The sutures in the area are not perfectly clear and it is impossible to tell whether or not such is the case.

SOLENHOFEN SPECIMEN

The medial portion of this fenestra, that bordered by the exoccipital, forms a median notch for the *vena cerebralis posterior* and the vagus and accessory nerves (an incomplete *foramen jugulare posterius*). The canal for these structures runs anterodorsomedially along the anterior margin of the exoccipital to enter the *cavum cranii* through the *foramen jugulare anterius.* This foramen is surrounded by the exoccipital except anteriorly where the opisthotic enters its margin. Near the medial end of the canal, the exoccipital forms the floor of the large *fenestra perilymphatica* which leads anteriorly through the opisthotic. The latter forms its medial, dorsal, and lateral margins. Ventrolaterally the margin of the foramen is incomplete, exactly like the same margin of the *foramen jugulare posterius*; in both cases, the opisthotic and exoccipital just fail to make contact ventrolaterally.

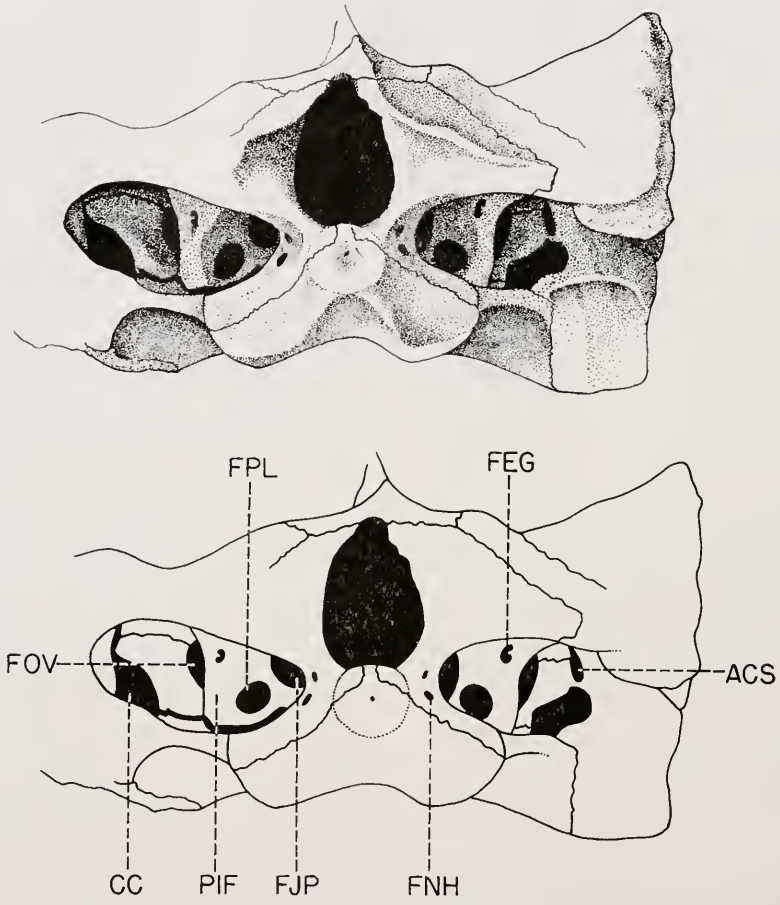

Fig. 6. Portland skull, British Museum R3164. Posterior view of skull fragment, modified to show both cava acustico-jugulares at comparable posterolateral angles. Abbreviations: ACS, aditus canalis stapedio-temporalis. CC, canalis cavernosus. FEG, foramen externum nervi glossopharyngei. FJP, foramen jugulare posterius. FNH, foramen nervi hypoglossi. FOV, fenestra ovalis. FPL, fenestra perilymphatica. PIF, processus interfenestralis.

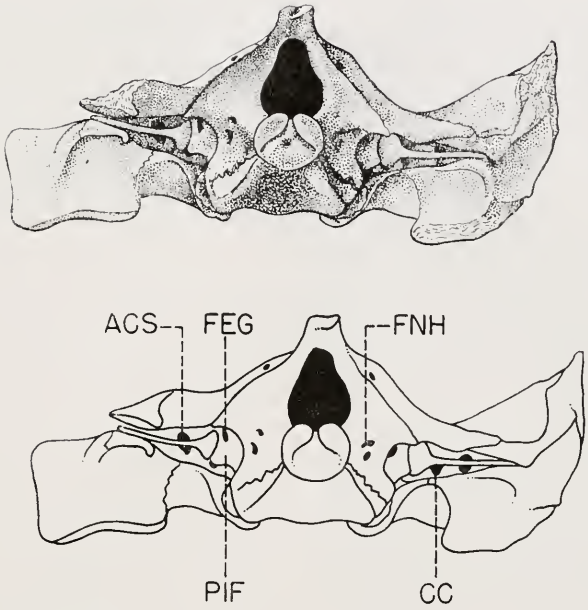

Fig. 7. Solenhofen skull, Teyler Museum. Posterior view. Abbreviations: ACS, aditus canalis stapedio-temporalis. CC, canalis cavernosus. FEG, foramen externum nervi glossopharyngei. FNH, foramen nervi hypoglossi. PIF, processus interfenestralis.

Os supraoccipitale

Much of the posterodorsal part of the supraoccipital is missing in all the specimens. There was at least some vertical portion which rose to meet the parietals; however, whether the supraoccipital actually formed any part of the dorsal roof or possessed any *crista supraoccipitalis* cannot be determined.

The supraoccipital forms the roof of the posterior part of the *cavum cranii* and of the otic region and the posteromedial portion of the floor of the *fossa temporalis* where it is bounded anteriorly by the parietal, anterolaterally by the proötic, and posterolaterally by the opisthotic. At its posterior end the supraoccipital possesses a short suture with each exoccipital and, between them, forms a narrow part of the dorsal margin of the *foramen magnum.* Within the *cavum cranii,* the supraoccipital is bounded by the same elements; between its sutures with the proötic and opisthotic it forms the dorsal margin of the large *hiatus acusticus.*

PORTLAND SPECIMENS

The details of the otic region can be studied, in part, in the fragmentary specimen (R3163). Apparently the supraoccipital forms very little of the roof of the *cavum labyrinthicum*; the *recessus labyrinthicus supraoccipitalis* is a very small cavity, probably containing only the *crus commune*. It is represented by a depression in the ventral surface of the supraoccipital. From this there is a canal leading anteriorly into the proötic for the *canalis semicircularis anterior* and another leading posteriorly to enter the opisthotic. The latter contained the *canalis semicircularis posterior*. There appears to be no *foramen aquaducti vestibuli*; a small notch is visible in the dorsal rim of the *hiatus acusticus*, but it may be the result of wear.

SOLENHOFEN SPECIMEN

The details of the otic region are obscure in the articulated skull. Certainly there is within the supraoccipital or neighboring bones a well developed *recessus labyrinthicus supraoccipitalis*. Nothing can be seen of the semicircular canals.

Os opisthoticum

The opisthotic is a roughly triangular element, the dorsal side of which forms the posterior end of the floor of the *fossa temporalis*. Dorsally it is bounded anteromedially (along the shortest side of the triangle) by the supraoccipital. The posterior edge possesses a suture with the exoccipital medially, but laterally it enters the posterior margin of the skull and the roof of the *fenestra postotica*. The exoccipital-opisthotic suture is long in the Portland skulls, but greatly shortened in the Solenhofen specimen. Most of the anterolateral margin of the opisthotic (the longest side of the triangle) is bounded by the quadrate; laterally the opisthotic also is in contact with the squamosal, especially in the Solenhofen skull. The anterior angle of the opisthotic just touches the proötic, but does not extend anterior as far as the *foramen stapediotemporale*. There is a much smaller foramen at the spot where the opisthotic, proötic, and quadrate meet; it could not be probed with a bristle. The dorsal surface of the opisthotic slopes gradually from a more dorsal position medially to a more ventral one laterally. Its posterior margin is somewhat ventral to its anterior one in the Portland skulls, but not in the Solenhofen form.

The lateral half of the ventral face of this element is a flat surface roofing much of the *cavum acustico-jugulare*; medially it becomes far more complex. A prominent *processus interfenestralis* extends anteroventrally from the main plate of bone, separating the more anterior *cavum labyrinthicum* from the more posterior canal for the *vena cerebralis posterior*. The process is thus a flat plate lying in the transverse plane. The small *foramen externum nervi glossopharyngei* pierces this process well dorsally; its posterior end is near the lateral margin of the process, and its anterior near the center so that the opening runs laterally as well as posteriorly. Near its lateral end the *processus interfenestralis* forms the anterior margin of the *foramen jugulare posterius* and the posterior margin of the *fenestra ovalis*, while medially the process forms the anterior boundary of the *foramen jugulare anterius* and the posterior boundary of the *hiatus acusticus*.

PORTLAND SPECIMENS

The ventral end of the process is sutured to the exoccipital medially and to the pterygoid laterally. Near its medial end, the ventral margin is pierced by the large *fenestra perilymphatica*; whether this fenestra is completely surrounded by the opisthotic or whether the exoccipital enters its ventral margin cannot be determined. The anteromedial margin of the *processus interfenestralis* is notched ventrally, possibly for the passage of the glossopharyngeal nerve. The notch may thus be an incomplete *foramen internum nervi glossopharyngei*.

In R3163 the interior of the *cavum labyrinthicum* may be seen. There is, in the anterior face of the opisthotic, a large posterodorsal recess of the *cavum labyrinthicum*, the *recessus labyrinthicus opisthoticus*; it is a roughly hemispherical cavity. The *canalis semicircularis posterior* leads from its posterodorsal wall into the supraoccipital.

SOLENHOFEN SPECIMEN

The ventral end of the process meets the exoccipital. Lateral to their contact there is a very large notch for the *fenestra perilymphatica*. The ventrolateral end of the process fails to reach the exoccipital or pterygoid so that the ventral margins of the *foramen jugulare posterius* and *fenestra perilymphatica* are incomplete. There is a small *foramen internum nervi glossopharyngei* in the anteromedial margin of the *processus interfenestralis* which leads from the *cavum labyrinthicum* to the *cavum cranii*.

Nothing can be seen of the inside of the *cavum labyrinthicum*; as in all turtles, the opisthotic here forms its posterior wall.

PORTLAND SPECIMENS

Anterolaterally there is a wider foramen for the *canalis semicircularis horizontalis*. The latter runs anteriorly to enter the large *recessus labyrinthicus proöticus*; the canal is separated from the *cavum labyrinthicum* only by a narrow bar of the opisthotic and is not bounded medially by the proötic at any point.

Internally the opisthotic is bounded by the supraoccipital dorsally and the proötic anteriorly. Its ventral margin roofs the *fenestra ovalis*.

Os proöticum

The proötic is a fairly small, irregularly shaped element lying in the anteromedial portion of the otic region. Its dorsal surface is a four-sided plate forming the anteromedial quarter of the floor of the *fossa temporalis*. Posteromedially it possesses a short suture with the supraoccipital and medially an equally short one with the *processus inferior parietalis*. Its longer anterior border forms the anterior margin of the floor of the *fossa temporalis*, including at least half of the prominent, spout-shaped *processus trochlearis*. There is a long posterolateral suture with the quadrate. Near the posteromedial end of this suture, the quadrate and proötic are separated by the large *foramen stapedio-temporale*. The foramen leads into a short but wide *canalis stapedio-temporalis* which runs ventrolaterally between the same two bones to open into the dorsolateral corner of the *cavum acustico-jugulare*, immediately dorsal to the posterior end of the *canalis cavernosus*.

PORTLAND SPECIMENS

The proötic forms roughly half to two-thirds of the moderately large *processus trochlearis*. Anteroventrally, it is bounded by the quadrate and has only a small exposure on the surface of the skull. The *processus inferior parietalis* sends a thin extension ventrally which meets the pterygoid posterior to the *foramen nervi trigemini*, thus

SOLENHOFEN SPECIMEN

The proötic forms nearly all of the exceedingly well developed *processus trochlearis*. Anteroventrally, it is bounded by the quadrate and, medially, by the pterygoid. The proötic enters the posterodorsal margin of the *foramen nervi trigemini*, and thus narrowly separates the *processus inferior parietalis* from the pterygoid.

PORTLAND SPECIMENS

excluding the proötic from the margin of that foramen. Whether or not the parietal and quadrate are in contact and separate the pterygoid and proötic posterior to the foramen cannot be determined with certainty, but it seems probable.

The lateral surface of the proötic forms the dorsolateral wall of the *canalis cavernosus* and of its anterior opening into the *cavum cranii*, the *foramen cavernosum*. Near its ventral border it is pierced by the *foramen nervi facialis* which enters the *canalis cavernosus*.

PORTLAND SPECIMENS

Just ventral to this foramen in R3163, the small *foramen pro ramo nervi vidiani* passes between the proötic and the pterygoid before entering the latter bone to emerge in the *canalis caroticus internus*.

SOLENHOFEN SPECIMEN

This foramen may be seen through the *foramen magnum*, but could not successfully be probed. Whether or not a *foramen pro ramo nervi vidiani* is present cannot be determined.

On its medial surface, the proötic possesses sutures with the basisphenoid ventrally, the supraoccipital posterodorsally, and the parietal anterodorsally. Posteriorly it forms the anterior margin of the *hiatus acusticus* and, anteriorly, its free surface is notched medial to the *foramen nervi trigemini*. Near its ventral end there is a conspicuous depression in the surface of the bone, the *fossa acustico-facialis*. The medial end of the *foramen nervi facialis* lies in the antero-ventral corner of this fossa.

PORTLAND SPECIMENS

Posterodorsal to the *foramen nervi facialis*, there is a single, fairly large *foramen nervi acustici*. Since the posterior margin of the proötic is somewhat eroded, it cannot be definitely stated that there was only one such foramen; however, there is no evidence for any others. In posterior view, the proötic possesses a ventromedial suture with the basisphenoid and a ventrolateral one with the pterygoid. Laterally it forms the dorso-

SOLENHOFEN SPECIMEN

Near the posterior margin of the fossa, there is a very small foramen, presumably a *foramen nervi acustici*. Other details of the medial surface of the proötic cannot be seen in this specimen. The posterior face of this bone is also mainly obscured. It possesses sutures with the basisphenoid ventromedially, the pterygoid ventrolaterally, the quadrate laterally, and the opisthotic dorsolaterally. The last two sutures are separated by the *aditus*

PORTLAND SPECIMENS

medial wall of the *canalis cavernosus* and, dorsally, possesses a suture with the quadrate. The last suture is interrupted by the *aditus canalis stapedio-temporalis*. Dorsally, it meets the opisthotic.

Much of the posterior wall of the proötic is hollowed out to form the large *recessus labyrinthicus proöticus*. This recess receives anterodorsally the *canalis semicircularis horizontalis*. The posteroventral margin of the recess forms the anterior and anteroventral borders of the *fenestra ovalis*.

SOLENHOFEN SPECIMEN

canalis stapedio-temporalis, and those with the pterygoid and the quadrate by the *canalis cavernosus*. The anterior margin of the *fenestra ovalis* is formed by the posterior edge of the proötic between its sutures with the basisphenoid and opisthotic.

The anterior wall of the *cavum labyrinthicum* is formed by the proötic; it cannot be seen in this specimen.

Os quadratum

This quadrate is a rather large, irregularly shaped element much like that of modern turtles. Its triangular dorsal surface forms most of the lateral half of the floor of the *fossa temporalis*. This surface is bounded posteromedially by the opisthotic, anteromedially by the proötic, and, along the posterior half of its lateral margin, by the squamosal. In the Solenhofen form, the anterolateral margin of the quadrate is bounded by another (unidentifiable) bone of the skull roof. However, in the Portland form the lateral margin is not perfect on any of the specimens; whether or not it was joined to any of the dermal elements of the skull roof cannot be determined. At its anteriormost extremity, the quadrate forms about a third of (in the Portland skulls) or just barely enters (in the Solenhofen) the lateral side of the *processus trochlearis* which is described above.

The medial wall of the quadrate is concave, and forms the lateral wall of the *cavum acustico-jugulare* posteriorly and of the large *canalis cavernosus* anteriorly. Ventral to these cavities, there is a suture between the pterygoid and the quadrate; dorsal to them, the latter meets the opisthotic and proötic as on its dorsal surface. The *canalis stapedio-temporalis* runs anteromedially as well as dorsally in the quadrate-proötic suture from its aditus which opens into the *cavum acustico-jugulare* to the *foramen stapedio-temporale* which opens into the *fossa temporalis*. Anteriorly the quadrate is a fairly simple plate.

Along its dorsal margin, the quadrate forms the anterior edge of the floor of the *fossa temporalis* laterally and possesses a suture with the

proötic medially. This suture passes along the underside of the *processus trochlearis* so that the quadrate forms a considerable portion of the ventral surface of the process. The anteromedial margin of the quadrate, which is slightly anterior to its anterolateral margin, joins the pterygoid in a moderately short vertical suture. This suture turns sharply ventrolaterally and continues along the medial half of the ventral margin of the quadrate which thus rests on the posterior wing of the pterygoid. Although the pterygoid separates the quadrate from the epipterygoid, there is a groove along the surface of the pterygoid between these two elements which may have contained a cartilaginous *processus epipterygoideus* of the quadrate. The quadrate does not enter the margin of the *foramen nervi trigemini.*

PORTLAND SPECIMENS

Since the *processus trochlearis* is not exceptionally large, the anterior face of the quadrate is only slightly concave, being nearly vertical ventrally and sloping anteriorly near its dorsal end.

At its ventrolateral end, the quadrate extends a short distance ventrally as the *processus articularis.* The actual articulating surface (*condylus mandibularis*) is preserved in only one specimen; it is a small parallelogram with the long sides in the transverse plane and the shorter ones running posterolaterally at angles of approximately twenty degrees from the sagittal plane.

SOLENHOFEN SPECIMEN

With the extreme development of the *processus trochlearis,* the anterior face of the quadrate is approximately vertical in its ventral half, but turns sharply anteriorly and is nearly horizontal dorsally.

At its ventrolateral end, the quadrate forms a broad but very short *processus articularis.* This bears the large *condylus mandibularis,* a rather long ovate area with the long axis in the transverse plane and the lateral end wider than the medial. It is somewhat arched, and its lateral and medial ends are both ventral to its center.

In posterior view little of the quadrate can be seen. Part of its exposure in the floor of the *fossa temporalis* is visible as is the *processus articularis.* Between these two parts, the squamosal and opisthotic join dorsal to the *fenestra postotica* and the *incisura columellae auris*; the latter is described below.

In lateral view, most of the quadrate is occupied by the large *cavum tympani.*

PORTLAND SPECIMENS

The cavum is a rather shallow bean-shaped depression which is deepest posterodorsally. At the

SOLENHOFEN SPECIMEN

The cavum is a deep, nearly circular depression. Its greatest depth is dorsally and posterodors-

PORTLAND SPECIMENS

posterodorsal corner, there is a small opening between the quadrate and the squamosal; presumably it led into an *antrum postoticum*, but most of the squamosal is lost so that this cannot be determined. There is a deep and quite wide *incisura columellae auris* which forms the hilum of the bean-shaped cavum. It expands almost to the center of the quadrate, as seen in this view, from the posteroventral margin. The incisura continues as a deep groove along the posteroventral margin to join the larger medial indentation of the quadrate which forms the lateral wall of the *cavum acustico-jugulare*.

SOLENHOFEN SPECIMEN

ally where it extends posteriorly into the squamosal as the *antrum postoticum*. There is no distinct boundary between the antrum and the *cavum tympani*. The *incisura columellae auris* is deep, extending anterodorsally from the posteroventral margin of the quadrate to the center of the cavum, but it is very narrow. This slit-like incisura extends along the posteroventral surface of the quadrate from the lateral margin to enter the lateral wall of the *cavum acustico-jugulare*. Along the ventrolateral margin of the incisura, there is a prominent ridge on the quadrate, so that its posteroventral surface is quite concave.

Columella auris

PORTLAND SPECIMENS

The columella is unknown.

SOLENHOFEN SPECIMEN

The columella is a rather straight, thin rod of bone extending medially and somewhat anteriorly from the center of the *cavum tympani* to the *fenestra ovalis*, between the proötic and opisthotic. It lies in the *incisura columellae auris* laterally and then extends across the center of the *cavum acustico-jugulare*. Medially its end is expanded into an oval *basis columellae* which fills the *fenestra ovalis*. The long axis of the oval is posterodorsal to anteroventral. The *basis columellae* is a very low conical structure with the shaft of the columella arising from its center. Since the columella does not extend laterally to the lateral surface of

SOLENHOFEN SPECIMEN

the quadrate, it was presumably continued in cartilage as in modern forms.

Cavum acustico-jugulare

The *cavum acustico-jugulare* forms a rather large cavity in the posteroventral surface of the skull. It is widely open posteroventrally through the large *fenestra postotica*. This fenestra is bounded by the exoccipital medially and dorsomedially, by the opisthotic dorsally, by the quadrate laterally and ventrolaterally, and by the pterygoid ventrally. In the Solenhofen form, but not in the Portland one, the basioccipital enters its ventromedial margin between the exoccipital and the pterygoid. The cavum itself is largely roofed by the opisthotic, with the quadrate taking part laterally, the proötic anteriorly, and the exoccipital posteromedially. Its floor is formed by the pterygoid medially and the quadrate laterally; the proötic enters the floor anteriorly. In the Solenhofen skull, the pterygoid is somewhat emarginated posteriorly so that the floor is less extensive than in the Portland specimens. The cavum, and also the *fenestra postotica*, is essentially drop-shaped with the larger, rounded end medial. Laterally it tapers gradually, and is continuous with the comparatively narrow *incisura columellae auris*. This incisura extends laterally as a groove within the quadrate to enter the posteroventral margin of the *cavum tympani*.

The *cavum acustico-jugulare* is partially divided by the *processus interfenestralis* of the opisthotic into two parts, a smaller posteromedial and a larger anterolateral chamber.

PORTLAND SPECIMENS

Ventrally the process, which extends anteroventrally from the body of the opisthotic, is solidly fused to the floor of the cavum along the length of the opisthotic-proötic suture. It is a thin, nearly transverse plate of bone.

SOLENHOFEN SPECIMEN

The process extends ventrally and slightly anteriorly as a thin, nearly transverse plate of bone. It does not extend to the floor of the cavum, and thus the *foramen jugulare posterius*, *fenestra perilymphatica*, and *fenestra ovalis* are incomplete ventrally. Presumably there was a cartilaginous extension of the process which completed the margins of these openings; if this was the case, then the pattern is almost identical with that seen in the Portland skulls, and one description will suffice for both.

The smaller, posteromedial portion of the *cavum acustico-jugulare* is a short and rather wide tubular cavity leading medially to open into the *cavum cranii*. It lies between the exoccipital and the opisthotic. The lateral end of this cavity is the *foramen jugulare posterius* and the medial end, opening into the cranial cavity, is the *foramen jugulare anterius*. Two smaller foramina enter the anterior (opisthotic) wall of the canal from the *cavum labyrinthicum*: dorsolaterally the small *foramen externum nervi glossopharyngei* and ventromedially the larger *fenestra perilymphatica*. Thus this passage serves for the transmission of the glossopharyngeal, vagus, and accessory nerves and a small vein (*vena cerebralis posterior* = *vena jugularis interna* of mammals), and is homologous with the jugular foramen of mammals.

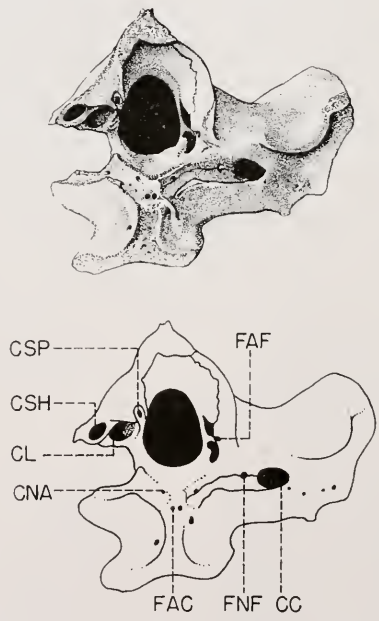

Fig. 8. Portland skull, British Museum R3163. Anterior view of skull fragment. Abbreviations: CC, canalis cavernosus. CL, cavum labyrinthicum. CNA, canalis nervi abducentis. CSH, canalis semicircularis horizontalis. CSP, canalis semicircularis posterior. FAC, foramen anterior canalis carotici interni. FAF, fossa acustico-facialis. FNF, foramen nervi facialis.

The larger, anterolateral portion of the *cavum acustico-jugulare* has three large openings which are separated from each other by the proötic. Dorsomedially there is a large circular *fenestra ovalis* which lies between

the proötic and the opisthotic. It opens into the *cavum labyrinthicum* and is occupied by the *basis columellae*. From this, the shaft of the columella extends laterally across the *cavum acustico-jugulare* and into the *incisura columellae auris*. Lateral to the *fenestra ovalis*, between the proötic and the quadrate, there is a smaller foramen, the *aditus canalis stapedio-temporalis*. The *arteria stapedialis* passes dorsally through it to reach the *fossa temporalis*. Finally, ventral to the two openings described above, there is the large posterior end of the *canalis cavernosus*. This canal runs posteriorly and somewhat laterally from the *cavum cranii* and contains the *vena capitis lateralis*. It is bounded by the quadrate laterally, the proötic dorsomedially, and the pterygoid ventromedially.

Cavum labyrinthicum

The *cavum labyrinthicum* forms a relatively large chamber containing the inner ear. It lacks, in the bony skull, a medial wall and is widely open into the *cavum cranii* through the *hiatus acusticus*. Presumably in life this hiatus was, as in recent turtles, almost entirely closed by cartilage. Although basically rectangular, the margin of the hiatus is very irregular; since this irregularity has been increased by erosion of the skulls, the details of its form are not worth elaborate description. Dorsally the hiatus is bordered by the supraoccipital, anteriorly by the proötic, ventrally by the basisphenoid, and posterodorsally by the opisthotic. Posteroventrally both the basioccipital and exoccipital also enter its margin in the Solenhofen skull; the same is true of one of the Portland skulls (R3164), but in another larger one (R2914) the opisthotic appears to extend ventrally to meet the basisphenoid and thus exclude both the basioccipital and exoccipital from the margin of the hiatus.

The *cavum labyrinthicum* is bounded posteriorly and posterolaterally by the *processus interfenestralis* of the opisthotic and anteriorly and anterolaterally by the proötic. These same two bones form the posterolateral and anterolateral thirds of the roof of the cavum. Between them and medial to them, the supraoccipital possesses a triangular exposure forming the medial third of the roof. Finally the ventral surface of the cavum is formed in large part by the pterygoid with the proötic and basisphenoid entering its anterolateral and medial sides respectively; their exposure in the floor of the cavum is larger in the Solenhofen than in the Portland form. In the latter, but not the former, the opisthotic also enters this floor posterolaterally.

Besides the *hiatus acusticus*, there are five other openings into the *cavum labyrinthicum* which can be seen in the specimens. Three of these, the *fenestra perilymphatica, foramen externum nervi glossopharyngei,* and *fenestra ovalis*, enter the *cavum acustico-jugulare* as described above.

They lie, respectively, ventromedially on the posterior wall, dorsolaterally on the posterior wall, and ventrally on the lateral wall of the *cavum labyrinthicum;* the first two are surrounded (or nearly so) by the opisthotic while the last is between the opisthotic and proötic. The *foramen internum nervi glossopharyngei* pierces the opisthotic between the *cava labyrinthicum* and *cranii,* and lies near the center of the posterior margin of the *hiatus acusticus.* Although present as a foramen in the Solenhofen skull, it is represented only by a small incisure in the margin of the opisthotic in the Portland form; presumably cartilage completed the margin of this small foramen. The *foramen nervi acustici* also connects the *cava labyrinthicum* and *cranii,* but it enters the anteromedial portion of the former, piercing the proötic. It is apparently a single foramen in both forms. Although there is no *foramen aquaducti vestibuli,* the supraoccipital (dorsal) margin of the *hiatus acusticus* is slightly notched; possibly the notch represents this foramen, but it is impossible to determine whether it is natural or a result of erosion of the skull.

PORTLAND SPECIMENS

The inside of the *cavum labyrinthicum* can be seen in only one specimen (R3163); the following description is based wholly on that one. There are, extending out posterolaterally, dorsally, and anteriorly from the dorsal part of the cavum, three prominent recesses, the *recessi labyrinthici opisthoticus, supraoccipitalis,* and *proöticus* respectively. They lie within the bones whose names they bear. The proötic recess, which presumably contained the *ampullae* of the *canales semicirculares anterior* and *horizontalis,* is the largest; the opisthotic recess which contained the third ampulla is larger than the supraoccipital recess. As in most recent turtles, all three semicircular canals lie, at least partially, within separate canals in the bones. Thus the *canales semicirculares anterior* and *posterior* run from the

SOLENHOFEN SPECIMEN

Almost nothing can be seen of the interior of the *cavum labyrinthicum,* and description is, therefore, not possible.

PORTLAND SPECIMENS

recessus labyrinthicus supraoccipitalis to the *recessi labyrinthici proöticus* and *opisthoticus* respectively, passing through the supraoccipital and the proötic or opisthotic. The third canal, the *canalis semicircularis horizontalis,* runs from the opisthotic to the proötic recess, but is surrounded only by the former bone.

Cavum cranii

The *cavum cranii* will be described but briefly; further details are given in the descriptions of the individual bones that surround it. Only that portion of the cavity posterior to the orbital region is considered here. Thus the cavity extends from the *foramen magnum* at its posterior end to the anterior margin of the *processus inferior parietalis.* Dorsally the cavum is roofed by the supraoccipital posteriorly and the parietal anteriorly. This roof is somewhat arched, being lowest posteriorly, and it is not pierced by any foramina.

The ventral surface of the cavum is considerably more complex. Most of it is formed by the dorsal surface of the basisphenoid, but its posterior quarter is composed of the basioccipital medially and the exoccipitals laterally. The pterygoid enters the floor of the cavum anterolaterally, along the ventral side of the *sulcus cavernosus.* For the posterior three-quarters of its extent this floor is a simple trough. In the Portland form, there is a moderately prominent *crista dorsalis basioccipitalis* at the anterodorsal end of the basioccipital; this crista is much reduced in the Solenhofen skull. A small *canalis nervi abducentis* runs anteroventrally through the basisphenoid from near its center on either side to enter the anterior part of the *sulcus cavernosus.* The posterior portion of the cranial floor ends at the *dorsum sellae.*

Anterior to this, the floor, formed by the *rostrum basisphenoidale,* continues as a horizontal trough, but at a lower (more ventral) level than farther posteriorly. The *dorsum sellae,* where the change in level occurs, is described in the section on the basisphenoid; it is pierced by the *foramen anterior canalis carotici interni* where the *arteria carotis interna* enters the *cavum cranii.* Lateral to the *rostrum basisphenoidale* there is a deep groove, the *sulcus cavernosus,* in which the *vena capitis lateralis* lies. Posterior to the *canalis nervi abducentis,* the vein passes through the *foramen cavernosum,* which lies lateral to the anterior margin of the

proötic, and hence leaves the *cavum cranii*. Immediately anterior to the *dorsum sellae* and *foramen anterior canalis carotici interni* is the *sella turcica* in which rests the pituitary; the sella is not markedly differentiated from the remainder of the anterior half of the cranial floor.

Seven bones enter the lateral wall of the *cavum cranii*. Dorsally it is formed by the ventral part of the supraoccipital and the *processus inferior parietalis*. Its ventral half consists of the exoccipital, the opisthotic (*processus interfenestralis*), the proötic, and the epipterygoid, in

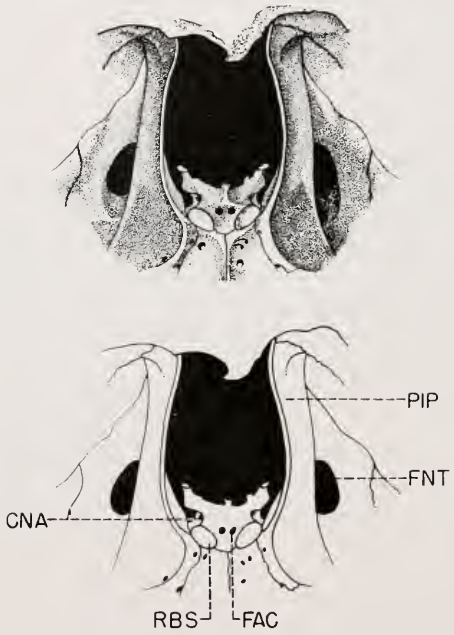

Fig. 9. Portland skull, British Museum R3164. Anterior view of region of dorsum sellae. Abbreviations: CNA, canalis nervi abducentis. FAC, foramen anterior canalis carotici interni. FNT, foramen nervi trigemini. PIP, processus inferior parietalis. RBS, rostrum basisphenoidale.

order from posterior to anterior. The *crista pterygoidea* enters the extreme ventral margin of the anterior quarter of the lateral cranial wall. This wall is penetrated by a series of foramina, mostly for the passage of all but the four most anterior cranial nerves (the canal for the abducens is more ventral and has already been mentioned). Posteroventrally the hypoglossal nerve exits through two small *foramina nervi hypoglossi* which are surrounded by the exoccipital. Slightly anterodorsal to these,

between the exoccipital and the opisthotic, lies the larger *foramen jugulare anterius;* through it pass the vagus and spinal accessory nerves as well as a small vein to enter the *cavum acustico-jugulare.* The opisthotic and proötic are separated by the large *hiatus acusticus* described above. In the Portland form its posterior margin is notched and in the Solenhofen skull there is a small foramen in the opisthotic just posterior to it, the *foramen internum nervi glossopharyngei.* The supraoccipital or dorsal margin of the hiatus may also have a small notch, presumably for the endolymphatic duct; this notch was probably made into a *foramen aquaducti vestibuli* by the cartilage which, in life, closed the *hiatus acusticus.* Both these notches and the hiatus enter the *cavum labyrinthicum.* Just anterior to the ventral part of the hiatus, there is a marked depression in the proötic, the *fossa acustico-facialis.* From this fossa a single *foramen nervi acustici* leads posterolaterally into the *cavum labyrinthicum.* Other foramina for the acoustic nerve may have been present in the cartilage mentioned above. Another foramen, the *foramen nervi facialis,* runs anteroventrally as well as laterally from the *fossa acustico-facialis,* just anteroventral to the *foramen nervi acustici.* It serves for the passage of the facial nerve and enters the *canalis cavernosus.* Finally the large oval *foramen nervi trigemini* lies well anteriorly, between the *processus inferior parietalis* and the *crista pterygoidea.* In the Portland form the foramen is completely surrounded by these two elements, but in the Solenhofen skull they are separated anteriorly by the epipterygoid and posteriorly by the proötic so that all four bones enter the margin of this foramen. Through it pass the maxillary and mandibular branches of the trigeminal nerve.

Mandible

Os dentale

The dentary is a large element forming most of the anterior half of the mandible. The long symphysis is solidly fused. Laterally the surface of the bone is slightly roughened, and possesses a series of nutritive foramina, most of them near its dorsal margin.

PORTLAND SPECIMENS

The anterior end of the dentary extends dorsally to form a gently curved, but quite strong beak. On the lateral edge of the triturating surface, there is a prominent labial ridge which is quite wide and blunt posteriorly, but becomes narrower

SOLENHOFEN SPECIMEN

The anterior end of the dentary is not upturned, and there are no ridges on the triturating surface. However, the labial margin of that surface is quite sharp. The symphysis is fully half the length of the entire dentary, thus forming a

PORTLAND SPECIMENS

and sharper anteriorly. Separated from the labial ridge by a deep trough, there is a well developed, sharp lingual ridge. The lingual ridges of either side meet near the middle of the long symphysis, and do not continue to the anterior end of the jaw. There are numerous small nutritive foramina within the trough between the ridges. The medial surface of the dentary, between the splenial and the symphysis, is deeply grooved by the *sulcus cartilaginis meckelii;* the sulci of opposite sides are continuous around the posterior end of the symphysis.

SOLENHOFEN SPECIMEN

large, relatively plane area which does, however, possess a distinct elongate median concavity occupying most of its length. There are numerous, fairly large nutritive foramina on the triturating surface, mostly just inside the labial margin. Medially, the splenial extends anteriorly nearly to the symphysis so that the *sulcus cartilaginis meckelii* is very short.

Posterolaterally, the jaws are broken, and the relationships cannot be fully determined. In medial view, the posterior half of the dentary is overlain dorsally by the coronoid and more ventrally by the splenial. Ventral to the latter element, the dentary extends posteriorly for an unknown distance; this region is eroded and the sutures between the elements cannot be seen.

Os spleniale

The splenial is a relatively large, plate-like bone on the medial surface of the mandible. It lies medial to the *sulcus cartilaginis meckelii*, and, in the Portland form, also ventral to its anterior portion. Thus the sulcus is really better termed a *canalis cartilaginis meckelii* for most of its length.

PORTLAND SPECIMENS

The splenial is a trapezoidal plate bounded dorsally by the coronoid, posterodorsally by the prearticular, ventrally by the dentary (and probably also by the angular which is too eroded to be identified), and anterodorsally by the *sulcus cartilaginis meckelii*. There is a foramen, presumably entering the Meckelian canal, near the anterior end of the splenial.

SOLENHOFEN SPECIMEN

The splenial is a diamond-shaped plate bounded anterodorsally by the coronoid, posterodorsally by the prearticular, posteroventrally by the angular, and anteroventrally by the dentary. Dorsal to the anterior point of the diamond, which nearly reaches the symphysis, is the opening of the short *sulcus cartilaginis meckelii*.

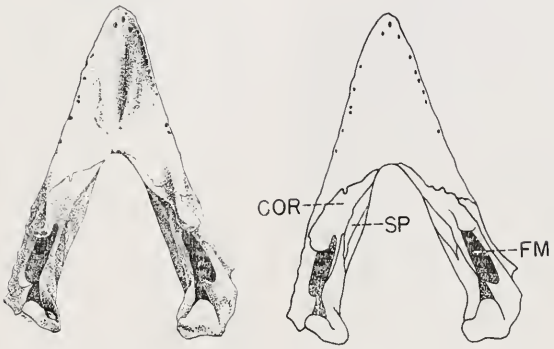

Fig. 10. Solenhofen mandible, Teyler Museum. Dorsal view. Abbreviations: COR, coronoid. FM, fossa meckelii. SP, splenial.

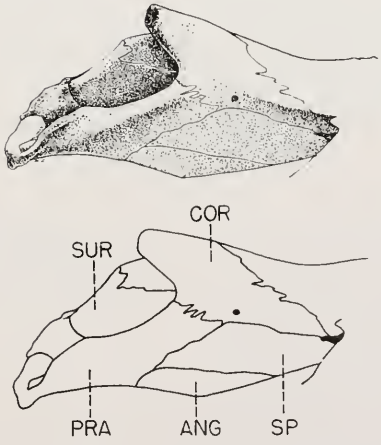

Fig. 11. Solenhofen mandible. Medial view of posterior end, left side. Abbreviations: ANG, angular. COR, coronoid. PRA, prearticular. SP, splenial. SUR, surangular.

Os coronoideum

PORTLAND SPECIMENS

The coronoid forms most of the moderately prominent *processus coronoideus*. Laterally it is exposed only at the tip of that process, but medially it appears as a large roughly triangular plate. It is bounded ventrally by the splenial anteriorly and by the prearticular posteriorly, and anterodorsally by the dentary. Near the anterior apex, there is a prominent foramen leading ventrolaterally into the bone, presumably to the *canalis cartilaginis meckelii*.

SOLENHOFEN SPECIMEN

The coronoid forms most of the very high and rather posteriorly directed *processus coronoideus*, thus having a considerable lateral exposure. Medially it appears as a rather long, narrow element bounded anterodorsally by the dentary and posteroventrally by the splenial and prearticular (with the first anterior to the second). The coronoid enters the triturating surface as a narrow splint of bone medial to the dentary; this extension reaches nearly to the symphysis. Near the center of its medial surface, the coronoid possesses a small foramen, presumably entering the *canalis cartilaginis meckelii*.

The posteroventral end of the coronoid is deeply and quite widely notched to form the anterodorsal margin of the *fossa meckelii*, and of the *canalis cartilaginis meckelii* which continues anteriorly from this fossa. Medial to the prearticular, a thin extension of the coronoid forms much of the medial wall of this fossa.

Os praearticulare

PORTLAND SPECIMENS

The prearticular is a plate of bone lying on the medial surface of the mandible ventral to the coronoid and posterodorsal to the splenial. Ventrally it meets an unidentifiable bone, probably the angular; this region is much eroded and little can be definitely determined. Posterodorsally it forms much of the medial margin of the *fossa meckelii*, although the coronoid partly separates the prearticular from the fossa.

SOLENHOFEN SPECIMEN

The prearticular is a rather long, thin element extending posteroventrally from its suture with the ventral margin of the coronoid. It is bounded anteroventrally by the splenial and, farther ventrally, by the angular. Although in medial view the prearticular appears to form the medial wall of the *fossa meckelii*, actually it is almost completely separated from that fossa by the thin posteroventral extension of the coronoid which lies

SOLENHOFEN SPECIMEN

along its medial surface. Posteroventrally the end of the prearticular is deflected medially and slightly expanded to form a surface facing posterodorsally and somewhat laterally. Although most of this surface is covered by the articular which rests on it and on the surangular, its anteromedial portion forms the medial end of the *area articularis mandibularis* which forms the mandibular articulation with the quadrate.

Os articulare

PORTLAND SPECIMENS

The articular is not preserved.

SOLENHOFEN SPECIMEN

The articular is a small triangular element bounded laterally by the surangular and medially by the prearticular; its posterior border is eroded. Its entire dosal surface forms, with the prearticular, the medial half of the *area articularis mandibularis* which articulates with the *condylus mandibularis* of the quadrate.

Os surangulare

PORTLAND SPECIMENS

The surangular is not preserved.

SOLENHOFEN SPECIMEN

The surangular is a bone on the lateral surface of the mandible very similar to the prearticular in its general relations. Anteriorly it forms the posterior half of the lateral wall of the *fossa meckelii*. Posterior to the fossa, the surangular becomes considerably thicker, possessing a medial extension which forms the concave posterior wall of the fossa. It also has a small lateral process at this level, but most of

SOLENHOFEN SPECIMEN

the lateral surface is eroded and its boundaries cannot be determined. The posterior end of the surangular expands to form nearly half of the *area articularis mandibularis*, the half which articulates with the lateral portion of the extended *condylus mandibularis* of the quadrate. The articular bone lies medial to the posterior end of the surangular. There is a small gap between the latter and the prearticular just anterior to the articular, and the posteromedial wall of the *fossa meckelii* is thus incomplete.

Os angulare

PORTLAND SPECIMENS

The angular is not preserved.

SOLENHOFEN SPECIMEN

The angular lies along the ventral margin of the posterior half of the jaw. This area is much eroded, especially laterally, and little can be seen. Medially it lies posteroventral to the splenial and anteroventral to the prearticular. Its ventral margin and lateral surface are not preserved, but the latter was probably quite extensive.

DISCUSSION: TURTLE SKULLS AND THE ORIGIN OF TURTLES

The interest which attaches to a turtle skull of Upper Jurassic age does not depend upon knowledge of the shell with which it was once associated or upon accurate knowledge of its systematic position and relationships. Interest in this case attaches to the antiquity of the fossil itself. A Jurassic turtle skull will manifest one of the grades of organization attained by the turtles during that period. It may not be (is not at all likely to be) unspecialized for that period, and one cannot be sure which are its specialized and which its primitive characters. Yet because of its relative closeness in time to the oldest turtles, it could be hoped that it would reveal a stage or step in the evolutionary line which stretches from the most ancient turtles to those of the Recent.

We are therefore disappointed to discover that two skulls of Upper Jurassic age tell us astonishingly little about the evolution of turtles, next to nothing about features primitive for turtles, and nothing at all that in any way points to the group from which turtles have been derived.

Old as they are, these skulls are of a modernized turtle type. There is no feature revealed by them that cannot be rather closely matched in some group of turtles still living. Four characters shared by the two Jurassic skulls are clearly primitive: the large splenial, the presence of nasals (inferred but not definitely shown in the Solenhofen skull), the widely exposed *fenestra postotica*, and the large epipterygoids. These characters are not found in combination in any later turtle, although each of them may still be met with in one or another of the surviving families. In most living turtles the splenial is absent or extremely reduced, and the nasals quite absent. The Chelidae, however, have splenials of moderate size (not indeed as large as in the Jurassic forms) and most members of this same family have nasals also. In most Recent turtles the *fenestra postotica* is partly or mostly walled off by secondary plates of bone, and in many Recent forms the columella is distally encircled by the quadrate, sometimes with considerable thickness of bone behind it. In the Recent sea turtles, on the other hand, the *fenestra postotica* is as widely exposed as in the two Jurassic turtles and the distal end of the columella is as loosely lodged in a notch of the quadrate as in the Portland form, less enclosed than in the Solenhofen skull. The epipterygoids are absent in both families of Recent Pleurodira — the Chelidae and the Pelomedusidae — and small in many

cryptodires, but other cryptodirous turtles have the epipterygoids almost as large as in the two Jurassic forms.

Each of the two Jurassic turtles presents peculiarities that do not seem to have any precise parallel in any other known turtle.

The palatal ridging of the Portland form is peculiar in that the inner maxillary ridge is exactly at the choanal border and is separated by a rather deep concavity from the tomial ridge. All Recent turtles in which a ridge is present at the choanal margin (e.g. the *Batagur* series of emydines and *Podocnemis*) have one or more ridges between the choanal ridge and the tomial one.

It is similarly the palate of the Solenhofen form that is somewhat peculiar. This, in contrast to the Portland form, has a strongly developed secondary palate. This is a specialized feature repeatedly developed in turtles; the Solenhofen palate is remarkable only in the reduction of the vomer which, while not vestigial or absent as in some *Podocnemis,* is completely concealed in palatal view, the maxillaries and palatines having met in a long suture beneath it. The closest approach to this condition is seen in the pelomedusids, none of which, however, are similar in detail.

We have then in these Jurassic species the quite familiar picture of more or less specialized primitive forms. They are not and they should not have been expected to be idealized diagrammatic ancestral types. They are end products in an early radiation of the turtles, but a radiation that occurred after turtles had assumed their definitive form — a form which they have kept basically unchanged into the Recent, though they have played infinite variations upon it.

The gap between these Jurassic turtles and the earliest known turtles, those of the Upper Trias, becomes very much more impressive now that these skulls are thoroughly known.

The shells of the Triassic turtles are very completely testudinate. They differ somewhat from the shells of Jurassic to Recent forms (which are actually somewhat simplified) but they are primitive only in a temporal sense, not in the sense of leading backward toward conditions and structures non-chelonian and ancestral.

The skull of *Proganochelys* (the one form in which a skull is known—*Triassochelys* is, we believe, a synonym) is quite different in this respect. The magnificent material at the Museum für Naturkunde at Stuttgart will be described in detail by Dr. K. Staesche. However, notes taken by and photographs furnished to one of us (E. E. Williams) while a Guggenheim Fellow in 1953 permit a few general remarks, in part confirming Jaekel's (1916) observations, in part emending them.

As Jaekel inferred, the narial opening was divided in *Proganochelys,* though his specimen did not show a complete septum. This division was accomplished, however, not as he imagined by a weakly calcified cartilaginous downward prolongation of the nasal (Jaekel, 1916, p. 152) but by dorsal processes of the premaxillae, the tips of which are inserted between the nasals much as in Recent lizards or ancient procolophonids (*Nycteroleter, Procolophon*, cf. Romer, 1956). In all other turtles, fossil and Recent, except *Kallokibotion*[1] of the Cretaceous of Transylvania, the nares are undivided.

The quadrate of *Proganochelys* is, as Jaekel pointed out, very different from that of all other turtles for which this bone is known. In place of the greatly developed *cavum tympani* and *incisura columellae auris,* already so typically shown in the Jurassic turtles that we have described, there is only a slight incurving of the quadrate — a faint indication of things to come. Apparently there was no notch whatsoever for the columella, and the tympanum must have been attached just to the posterior edge of the quadrate instead of being for the most part bounded by that bone. The condition seems as primitive as in many cotylosaurs and more primitive than in *Diadectes.*

The Stuttgart skulls show that the palate of *Proganochelys* was in some respects more primitive than Jaekel believed. In place of the "large tooth-bearing parasphenoid" of Jaekel's figure and text, the Stuttgart skulls show a distinct interpterygoid vacuity. Jaekel's specimen showed crushing in this area, and indeed he admits as much (1916, p. 175; see also his photograph, Tafel 5B). The photograph of a quite uncrushed skull (Pl. 5) shows the actual situation clearly; a cultriform process is plainly visible between the separated pterygoids. Posteriorly also the situation is primitive; the quadrate ramus of the pterygoid does not send any flange inward to floor the cranioquadrate passage as in all other known turtles, and the foramina for the *vena capitis lateralis,* the internal carotid, and the stapedial artery, as well as the *fenestra ovalis* are all exposed in ventral view. In all respects *Proganochelys* approaches the primitive reptilian condition and is separated by a very sizable morphological gap from such modernized turtles as the Jurassic ones we have described.

[1]Except in this regard, this peculiar, relatively late genus is not primitive. The material (seen in the British Museum) is poorly preserved, the sutures difficult to trace, and not made easier to see by the white paint with which Nopcsa marked them (sometimes changing his mind and incompletely removing a previously painted line). In certain places breaks and injury to the surface account for the peculiar course of some of the cranial sutures shown by Nopcsa (1923).

Currently the Jurassic families and many later turtles including some that survived to the Pleistocene (*Meiolania*) are united with the forms of the Trias in a suborder Amphichelydia. It is quite clear from what has been said above that the morphological gap is much greater between Triassic forms and all later ones than within the latter group. If major divisions below the order are to be made, the basic one obviously must be between the Triassic ones and all the others.

Indeed, *Proganochelys* fits Watson's (1914) concept of "Archichelone" better than *Eunotosaurus,* which Watson presented as a possible testudinate ancestor.

Seeley in 1892 and Watson much more elaborately in 1914 suggested *Eunotosaurus africanus* as a turtle ancestor. Watson's procedure was especially interesting in that he reasoned from the apparent agreement in many features of *Eunotosaurus* and a hypothetical "Archichelone" or theoretical turtle ancestor constructed by extrapolation from the characters of the turtles then known. His summary of the resemblances between *Eunotosaurus* and "Archichelone" was more plausible in 1914 than it appears to be now. The advance of our knowledge, both of living and fossil turtles, and especially the discovery and description by Jaekel (1916) of *Triassochelys* only shortly after the appearance of Watson's paper, has, not surprisingly, required some revision of his ideas. For the most part these revisions indicate greater primitiveness for "Archichelone" than Watson was quite prepared to admit.

We may with more confidence comment on these points since one of us (E. E. Williams) in 1952 and 1953 while visiting Europe as a Guggenheim Fellow examined the material of *Eunotosaurus* at the British Museum only a few months before seeing the fabulously fine Triassic turtles at Stuttgart. The latter were only briefly studied, but we may in consequence use the description by Jaekel of *Triassochelys* with greater confidence.

It will be useful to compare Watson's concept of "Archichelone" with a more modern version of the same concept based on *Proganochelys-Triassochelys* and with the *verifiable* characters of *Eunotosaurus.* An examination of the British Museum *Eunotosaurus* leads one to sympathize with the observation of Broom (1941), who stated: "I have examined the specimens in the British Museum and three or four other specimens which are a little better preserved than these, but I have never published any descriptions of them, always hoping that a really good specimen will be found."

We will follow the procedure of first stating Watson's prediction of the characters of "Archichelone," following this with a version modified in accordance with more recent knowledge, and then compare the latter with *Eunotosaurus*.

SKULL. Watson: " 'Archichelone' had a roofed skull with a primitive Reptilian palate, teeth, probably only a squamosal of the temporal series and no facial (internarial) processes of the premaxillaries . . ."

Revised statement. Watson's summary holds good with minor modifications. Jaekel (1916) has, somewhat doubtfully, described a supratemporal in *Triassochelys*. Olson (1947 and 1950) would prefer to call the questioned bone in *Triassochelys* an intertemporal. In all later turtle types only one bone of the temporal series, usually regarded as the squamosal, is ever present. The absence of internarial processes also does not antedate the definitive differentiation of turtles. They were present in the oldest turtles, as reported by Jaekel. Two skulls of *Proganochelys* also show this internarial septum (originals seen at Stuttgart, a cast in the British Museum). Nopcsa (1923) has described a complete internarial septum in the much later (Cretaceous) turtle *Kallokibotion*. One of us (E.E.W.) has seen the skull of this form in the British Museum and can confirm Nopcsa's observations.

Eunotosaurus. Extremely little of the skull is known. Portions of the jaws and of the palate [1] are preserved, in each case very imperfectly. Except for the small size of the teeth, described by Watson as very small on the pterygoid, and only slightly larger on the maxilla and premaxilla, the palate so far as can be seen is merely primitive without special resemblance to that of turtles. Even in the case of the teeth there is a significant contrast. As appears from Jaekel's (1916) description, the teeth were extremely small on the maxilla and premaxilla in Triassic turtles and somewhat larger and more numerous on the pterygoid and vomer. As Broom (1941) has stated there are certainly more teeth on the maxillae of *Eunotosaurus* than Watson described. Watson believed that there was no internarial septum in *Eunotosaurus*.

NECK. Watson: " 'Archichelone' must have had a long and flexible neck. . . . As all known chelonians have eight cervical vertebrae, we are justified in claiming this number for 'Archichelone'."

[1] So little of the palate is visible that we would not ourselves choose to say anything about it.

Revised statement. The neck of 'Archichelone' was short, armored, and had no more than seven vertebrae. Jaekel (1916) has described a well-preserved cervical column in *Triassochelys*. In this the seven cervicals were short and amphicoelous with high spines, two-headed ribs, and large dermal ossicles in the skin above them. The eighth vertebra was still part of the trunk region and was added to the neck only in later types. This neck could have had only a very limited flexibility. Truly flexible and elongate necks did not evolve in turtles before the Cretaceous.

Eunotosaurus. In the one specimen of this form in which the skull is preserved, it is found with its ventral surface applied to the ventral surface of the trunk region, its anterior end pointing backward. Watson believed that this position was only possible if the neck were fairly long and flexible. To the extent that this conclusion is justified, we must regard *Eunotosaurus* as more specialized in the Permian than any turtle was before the Cretaceous. In fact, however, we know nothing about the neck of *Eunotosaurus*.

TRUNK. Watson: "'Archichelone' had a series of dorsal scutes comparable to those of a crocodile. . . . It is by no means unlikely that it resembled many members of that group in having ventral scutes not homologous with abdominal ribs."

Watson further believed that "Eight of ten dorsal vertebrae and their ribs have special relationships with dorsal and dorsolateral scutes, while the peripherals probably correspond to another set of bony scutes." Nuchal and pygal were probably originally connected with additional vertebrae in front of and behind the specialized ones and "lost this primitive connection after the formation of the shell."

Revised statement. Again certain corrections or qualifications need to be made. Many authorities believe that the major portion of the turtle plastron represents fused abdominal ribs. Jaekel, indeed, believed that signs of this origin were still present in *Triassochelys;* at all events in this genus a subdivision of the plastron into the relatively large paired units of later forms was not visible. Again while eight is the usual number of vertebrae involved in the shell in modern turtles, nine pleurals occur in a number of fossil forms including the oldest well-known types, *Triassochelys* = *Proganochelys*. One or more suprapygals occur in addition to these nine. On the other hand, the eighth cervical vertebra was fused to the nuchal in *Proganochelys* just as Watson anticipated might be the case in "Archichelone."

Eunotosaurus. There were ten dorsal vertebrae. Watson described them as follows: "these are all fairly similar in structure. The first is short, the second somewhat longer, and the third very long. The fourth, fifth and sixth are about as long as the third, and the seventh to tenth show progressive diminution in length. The structure of the individual vertebrae is best shown in the type specimen. The centrum is very slender, particularly in the fourth to seventh dorsals, and somewhat hour-glass shaped; it is completely pierced by the notochordal canal. The rib-facet is carried on a very low and small process which in the mid-dorsal region is placed at the extreme anterior end of the centrum, whilst anteriorly and posteriorly it travels back to the middle of its length. The neural arch is rather massive when compared with the centrum but still very narrow. It bears very narrow zygapophyses which seem to interlock strongly. The upper surface of the neural arch is essentially flat, being represented only by a low median ridge. The whole arch appears to be placed very far forward on the centrum and may overlap its anterior end. There is no definite transverse process but the ribs seem to touch the sides of the neural arch.

"The first dorsal rib is a narrow, slightly bent and quite short bone of an ordinary character. The remaining dorsal ribs, from the second to the ninth, are of an extraordinary character. Each is strongly curved, articulates by a facet on its proximal end with the facet on the centrum, and then rises, until its upper surface comes in contact with the neural arch; there is no definite tuberculum and the capitulum is extremely feeble. The rib then rises above the level of the neural spine so that the dorsal surface of the vertebral column lies at the bottom of a groove formed by the proximal ends of the ribs. The rib now turns outwards and downwards. The ribs widen very rapidly from the capitulum, so that until just at the point where they turn downwards their lateral borders actually touch. They are of a massive character throughout, and each is strengthened by the development of a ridge along its visceral surface."

There is in addition to these structures perhaps a dorsal bony armor above them, as Watson inferred from one specimen. Watson says: "In this individual in the anterior dorsal region a small patch of what is undoubtedly bone substance is shown lying a considerable distance above the ribs and neural arches. This is clearly divided into pieces, one of which forms a small round ridge in the middle line. The rest of the patch shows a dividing

line running longitudinally and a transverse division apparently coincident with the line where the two ribs below it meet. At the posterior end of the specimen, at the same distance above the ribs, a narrow line of bone is seen in transverse section. This specimen gives conclusive evidence of the actual presence of dermal ossifications, but these are so incompletely preserved as to make any statement of their distribution of very slight value. There seem, however, to have been a median series and lateral rows."

Broom (1941) describes the ribs a little differently: "The upper half of each rib is broad and convex above, but with a deep median keel, so that in section each rib is triangular. Further in most specimens the edges of the ribs do not meet but each rib overlaps the rib behind it. Then each rib has a long pointed lower half which passes downwards and slightly inwards. Each rib is singleheaded."

That there is here a parallel to the turtle condition is undoubtedly true; that it is a close parallel we do not believe. The semblance of a carapace is achieved by a broadening of the ribs themselves, so that they are already very wide close to their vertebral articulations. In all true turtles including *Proganochelys* the ribs themselves are not widened at all. From their articulations with the vertebrae to their point of entrance into the carapace they are not visibly very different from the ribs of more typical vertebrates. Their apparent width in the carapace and their close union with one another result from the addition to them of a dermal component in which they are embedded. The lack of width of the ribs themselves appears especially clearly when, as in several lines of marine turtles, the dermal component of the carapace is strongly reduced and the ribs appear as separate, narrow, well-spaced elements.

The pleural bone of a turtle is thus not pure cartilage bone and not merely a rib; it is the endochondral rib *plus* membrane bone ossified around it. Ruckes (1929) in a study of the development of the turtle carapace showed that the carapace is early represented by a thickening of the dermis with which the ribs and neural arches *secondarily* gain connection and which they organize into pleurals and neurals. The ribs and neural arches give a segmental character to the carapace, and they add a very firm internal support, but the carapace is, according to Ruckes, independent in its origin from the ribs and neural arches — originally a quite separate dermal thickening. Ruckes' observations have been confirmed by Walker (1947).

It is true that the situation in turtles is not simple. As Zangerl's (1939) study has emphasized, there are two layers of dermal ossification possible in turtles — a deep thecal layer and a superficial epithecal layer, but it is hardly possible to evade the conclusion that both layers are *dermal*[1] and that even the deeper one is in no sense part of the ribs. In addition, the epithecal layer seems to be a late development phyletically, unknown before the late Cretaceous.

In regard to the elongation of the dorsal vertebrae in *Eunotosaurus,* thought by Watson to be a resemblance to "Archichelone," it must be commented that the elongation is extreme in *Eunotosaurus,* greater than in many modern turtles and much greater in the middle Permian animal than in *Proganochelys* of the late Triassic.

LIMB GIRDLES. Watson: "In 'Archichelone' the pectoral girdle was undoubtedly in the usual position overlying the first dorsal ribs, and must have been narrow relative to the bulk of the trunk to allow of its passage back within the ribs. . . . The pelvic girdle must also have been very narrow."

Revised statement. Undoubtedly in the remoter ancestors of turtles the relation of shoulder girdle and ribs must have been of the normal vertebrate type, but the hypothesis that the girdles must have been narrow reflects a prior hypothesis as to the method by which the change in that relation came about. It may or may not be true.

Eunotosaurus. The limb girdles are primitive and small, but not especially prophetic of conditions in turtles.

LIMBS. Watson: "We may take it as probable that 'Archichelone' had limbs more or less like *Eryops* or *Varanosaurus* or *Dimetrodon.*" He mentioned, however, the narrow distal end of the humerus and the short powerful downwardly directed radial and ulnar crests of turtles and regards the presence of a shell as reasons for these. The rounded and upturned head of the humerus he described as "an obvious adaptation to the retraction of the limbs."

Revised statement. Von Huene (1926) has described a Triassic turtle humerus. It is much more primitive than any modern type, especially in the greater width of the distal end and the

[1]It has been suggested that the deeper layer is periosteal (Goette, 1899), but in fact the thickening of the dermis which is to include both layers of carapace bone occurs very early and is *not* a development of the perichondrium or periosteum.

general shortness and stoutness of the bone. It is otherwise, however, very evidently a turtle humerus with a head and ulnar and radial crests of a quite typical sort.

Eunotosaurus. The limbs are incompletely preserved but "the development of a short powerful ulnar crest on the humerus and the slight upturning of its head" are felt to be resemblances to turtles. It should be noted, however, that, as Watson feels these characters go along with the presence of a shell, they are resemblances implying affinity to turtles only if the shell truly indicates such an affinity.

To sum up, *Eunotosaurus* does show a number of resemblances to the turtles, but these resemblances are often to advanced types instead of to early and primitive members of the order. The apparent prototype of a chelonian carapace found in *Eunotosaurus* is in reality basically different in plan and is primarily interesting as *another* method by which a similar result may be achieved. Finally, the relation of limb girdles to ribs in *Eunotosaurus* is merely primitive and helps no more than do similar conditions in other groups in visualizing the way in which the strange condition so fundamental for turtles may have come about.

In thus dismissing *Eunotosaurus* we do not intend to disparage Watson's shrewdness and insight in estimating the characters of a turtle ancestor. We desire only to point out that in all its characters, *except its shell, Proganochelys* fits his concept or is more primitive than he felt justified in suggesting. In skull, neck, even limbs and girdles we are not justified in asking for a more primitive proto-turtle than the Triassic animals already provide. We may indeed associate the proto-turtle with that broad and varied group called Diadectomorpha, but it is at least the authors' feeling that an attempt to derive the turtles directly from any of the other diadectomorph groups fails, that the lineage of turtles goes down *alongside* the other lineages to somewhere close to the roots of the larger group itself. Turtles are, in fact, coordinate with the other diadectomorphs rather than derivative from them.

The shell of turtles and in particular its relation to the shoulder girdle remains an unsolved problem. It was this problem which Watson attempted to settle by utilizing *Eunotosaurus* as a turtle ancestor; in this, we believe, he did not succeed.

TERMINOLOGY

Unfortunately there is, at present, no standard system of anatomical terminology in general use for turtle skulls; almost every author who has described them has invented his own names for many structures. In the present work we have attempted to devise a fairly consistent terminology, using familiar terms whenever they are appropriate and coining new ones only when none of the previously proposed names seemed satisfactory. The following lists present the terms we have used and some of the more familiar of their synonyms. Four earlier papers (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; and Nick, 1912) are outstanding in the detailed description of turtle skulls, and all their terms equivalent to those used in the present paper are included. It will be noted that even in the case of the most familiar structures there has been little uniformity in the names used by these four authors. Other works are cited when they proposed or standardized the use of a term or a system of terms which is not used in any of the four major papers but which we have adopted. In many cases the authors cited were not the originators of the terms with which we have credited them. All those names for which no author is cited are original. This rather elaborate listing of terms is made in the hope, first, that it will be useful to future workers comparing the discussion in the previous papers on turtle skulls and, second, that it may bring about some standardization of such terminology.

Terms Used in the Present Work:

aditus canalis stapedio-temporalis
antrum postoticum (Williams, 1954)
apertura narium externa (Siebenrock, 1897; Ogushi, 1911)
apertura narium interna (Siebenrock, 1897)
area articularis mandibularis
basis columellae (Siebenrock, 1897)
canalis alveolaris superior (Ogushi, 1911)
canalis caroticus internus (Siebenrock, 1897)
canalis cartilaginis meckelii
canalis cavernosus (Siebenrock, 1897; Nick, 1912)
canalis nervi abducentis (Siebenrock, 1897)
canalis nervi vidiani (Siebenrock, 1897)
canalis semicircularis anterior (Kesteven, 1910; Ogushi, 1911; Nick, 1912)
canalis semicircularis horizontalis (Siebenrock, 1897)
canalis semicircularis posterior (Kesteven, 1910; Ogushi, 1911; Nick, 1912)
canalis stapedio-temporalis (McDowell, pers. comm.)

cavum acustico-jugulare (Kesteven, 1910)
cavum cranii (Nick, 1912)
cavum labyrinthicum (Ogushi, 1911)
cavum tympani (Siebenrock, 1897)
columella auris (Kesteven, 1910; Ogushi, 1911; Nick, 1912)
condylus mandibularis (Siebenrock, 1897)
condylus occipitalis (Siebenrock, 1897; Nick, 1912)
crista dorsalis basioccipitalis
crista pterygoidea (Siebenrock, 1897; Ogushi, 1911)
crista supraoccipitalis (Siebenrock, 1897; Nick, 1912)
dorsum sellae (Ogushi, 1911; Nick, 1912)
fenestra ovalis (Nick, 1912)
fenestra perilymphatica (Ogushi, 1911)
fenestra postotica (Nick, 1912)
fenestra subtemporalis (Romer, 1956)
fissura ethmoidalis (Kesteven, 1910)
foramen alveolare superius (Siebenrock, 1897)
foramen anterior canalis carotici interni
foramen aquaducti vestibuli (Siebenrock, 1897)
foramen cavernosum (Nick, 1912)
foramen externum nervi glossopharyngei (Nick, 1912)
foramen internum nervi glossopharyngei (Nick, 1912)
foramen jugulare anterius (Siebenrock, 1897; Nick, 1912)
foramen jugulare posterius (Siebenrock, 1897)
foramen magnum (Kesteven, 1910; Nick, 1912)
foramen nervi acustici (Siebenrock, 1897)
foramen nervi facialis (Siebenrock, 1897)
foramen nervi hypoglossi (Siebenrock, 1897)
foramen nervi trigemini
foramen orbito-nasale (Ogushi, 1911)
foramen palatinum posterius (Siebenrock, 1897)
foramen posterior canalis carotici interni
foramen praepalatinum (Seydel, 1896)
foramen pro ramo nervi vidiani (Siebenrock, 1897)
foramen stapedio-temporale
fossa acustico-facialis (Nick, 1912)
fossa meckelii (Siebenrock, 1897)
fossa nasalis
fossa temporalis (Siebenrock, 1897; Ogushi, 1911; Nick, 1912)
hiatus acusticus (Kesteven, 1910)
incisura columellae auris (Nick, 1912)
meatus choanae (Kesteven, 1910)
os angulare (Siebenrock, 1897; Ogushi, 1911; Nick, 1912)
os articulare (Siebenrock, 1897; Ogushi, 1911; Nick, 1912)
os basioccipitale (Siebenrock, 1897; Ogushi, 1911; Nick, 1912)
os basisphenoideum (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os coronoidum (Siebenrock, 1897; Nick, 1912)

os dentale (Siebenrock, 1897; Ogushi, 1911; Nick, 1912)
os epipterygoideum (Siebenrock, 1897; Kesteven, 1910; Nick, 1912)
os exoccipitale (Ogushi, 1911; Nick, 1912)
os frontale (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os jugale (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os maxillare (Siebenrock; 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os nasale (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os opisthoticum (Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os palatinum (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os parietale (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os postorbitale (Romer, 1956)
os praearticulare (Romer, 1956)
os praefrontale (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os praemaxillare (Siebenrock, 1897; Kesteven, 1910)
os proöticum (Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os pterygoideum (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os quadrato-jugale (Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os quadratum (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os spleniale (Romer, 1956)
os squamosum (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)
os supraoccipitale (Siebenrock, 1897; Ogushi, 1911; Nick, 1912)
os surangulare (Romer, 1956)
processus articularis (Siebenrock, 1897; Ogushi, 1911; Nick, 1912)
processus clinoideus (Siebenrock, 1897; Kesteven, 1910; Nick, 1912)
processus coronoideus (Ogushi, 1911)
processus epipterygoideus (Siebenrock, 1897)
processus inferior parietalis (Ogushi, 1911)
processus interfenestralis (Kesteven, 1910)
processus pterygoideus externus
processus trochlearis (Schumacher, 1954)
recessus labyrinthicus opisthoticus
recessus labyrinthicus proöticus
recessus labyrinthicus supraoccipitalis
rostrum basisphenoidale (Zangerl, 1953)
sella turcica (Ogushi, 1911)
sulcus cartilaginis meckelii (Siebenrock, 1897; Nick, 1912)
sulcus cavernosus (Siebenrock, 1897; Ogushi, 1911; Nick, 1912)
sulcus olfactorius (Kesteven, 1910)
sulcus vomeri (Ogushi, 1911)
tuberculum basioccipitale (Siebenrock, 1897; Nick, 1912)
vomer (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912)

Terms Used in Other Major Works:

ampulla canalis semicircularis frontalis (Siebenrock, 1897) = recessus labyrinthicus opisthoticus
ampulla canalis semicircularis sagittalis (Siebenrock, 1897) = recessus labyrinthicus proöticus

antivestibulum (Ogushi, 1911) = cavum acustico-jugulare (in part)
antrum mastoideum (Siebenrock, 1897) = antrum postoticum
canaliculus pro nervo abducente (Ogushi, 1911) = canalis nervi abducentis
canaliculus pro ramo communicante n. palatini (Ogushi, 1911) = foramen pro ramo nervi vidiani
canalis abducens (Kesteven, 1910) = canalis nervi abducentis
canalis arteriae temporalis posterior (Ogushi, 1911) = canalis stapedio-temporalis
canalis caroticus (Kesteven, 1910; Ogushi, 1911; Nick, 1912) = canalis caroticus internus
canalis caroticus externus (Siebenrock, 1897) = canalis stapedio-temporalis
canalis deuterencephalicus (Ogushi, 1911) = cavum cranii (in part)
canalis facialis (Kesteven, 1910; Ogushi, 1911; Nick, 1912) = foramen nervi facialis
canalis glossopharyngeus (Kesteven, 1910) = foramina externum et internum nervi glossopharyngei
canalis hypoglossi (Kesteven, 1910; Nick, 1912) = foramen nervi hypoglossi
canalis inframaxillaris (Ogushi, 1911) = canalis cartilaginis meckelii
canalis jugularis (Kesteven, 1910) = canalis cavernosus
canalis olfactorius (Ogushi, 1911) = sulcus olfactorius
canalis palatinum major et minor (Ogushi, 1911) = foramen palatinum posterius
canalis semicircularis externus (Nick, 1912) = canalis semicircularis horizontalis
canalis semicircularis frontalis (Siebenrock, 1897) = canalis semicircularis posterior
canalis semicircularis inferior (Kesteven, 1910) = canalis semicircularis horizontalis
canalis semicircularis lateralis (Ogushi, 1911) = canalis semicircularis horizontalis
canalis semicircularis sagittalis (Siebenrock, 1897) = canalis semicircularis anterior
cavitas glenoidalis (Ogushi, 1911) = area articularis mandibularis
cavum archencephalicum (Ogushi, 1911) = cavum cranii (in part)
cavum intermedium (Ogushi, 1911) = cavum acustico-jugulare (in part)
cavum nasi (Kesteven, 1910) = fossa nasalis
cavum tympani (Nick, 1912) = cavum tympani, antrum postoticum, and cavum acustico-jugulare
cavum tympanicum (Ogushi, 1911) = cavum tympani
choana (Siebenrock, 1897; Kesteven, 1910; Ogushi, 1911; Nick, 1912) = apertura narium interna
columella (Siebenrock, 1897) = columella auris
columella (Ogushi, 1911) = os epipterygoideum
complementare (Ogushi, 1911) = os coronoideum
crista basioccipitalis (Nick, 1912) = crista dorsalis basioccipitalis
crista occipitalis (Kesteven, 1910; Ogushi, 1911) = crista supra-occipitalis
crista praetemporalis (Siebenrock, 1897) = processus trochlearis
dorsum ephippii (Siebenrock, 1897) = dorsum sellae
fenestra rotunda (Kesteven, 1910) = fenestra perilymphatica
foramellum anterius pro nervo glossopharyngeo (Ogushi, 1911) = foramen internum nervi glossopharyngei
foramellum posterius pro nervo glossopharyngeo (Ogushi, 1911) = foramen externum nervi glossopharyngei
foramen acusticum (Nick, 1912) = foramen nervi acustici
foramen acusticum anteriore principale (Ogushi, 1911) = foramen nervi acustici

foramen alveolare superius anterius (Ogushi, 1911) = foramen alveolare superius
foramen arteriae facialis (Nick, 1912) = foramen stapedio-temporale
foramen carotico-temporale (Siebenrock, 1897) = foramen stapedio-temporale
foramen caroticum (Kesteven, 1910) = foramen anterior canalis carotici interni
foramen caroticum externum (Siebenrock, 1897) = aditus canalis stapedio-temporalis
foramen caroticum internum (Siebenrock, 1897) = foramina anterior et posterior canalis carotici interni
foramen carotidis internae (Nick, 1897) = foramen anterior canalis carotici interni
foramen cochleae (Siebenrock, 1897) = fenestra perilymphatica
foramen cribrosum anterius (Kesteven, 1910) = foramen nervi acustici
foramen externum nervi facialis (Nick, 1912) = foramen nervi facialis (in part)
foramen externum nervi hypoglossi (Nick, 1912) = foramen nervi hypoglossi (in part)
foramen incisivum (Siebenrock, 1897; Ogushi, 1911; Nick, 1912) = foramen praepalatinum
foramen internum nervi facialis (Nick, 1912) = foramen nervi facialis (in part)
foramen internum nervi hypoglossi (Nick, 1912) = foramen nervi hypoglossi (in part)
foramen jugulare internum (Siebenrock, 1897) = foramen cavernosum
foramen jugulare internum (Ogushi, 1911) = foramen jugulare anterius
foramen lacerum (Siebenrock, 1897; Ogushi, 1911) = fenestra postotica
foramen lachrymale (Kesteven, 1910) = foramen orbito-nasale
foramen narium externum (Ogushi, 1911) apertura narium externa
foramen nasopalatinum (Nick, 1912) = foramen orbito-nasale
foramen nervi abducentis (Nick, 1912) = canalis nervi abducentis
foramen nervi glossopharyngei (Siebenrock, 1897) = foramen externum nervi glossopharyngei
foramen nervi vidiani, ramus facialis (Siebenrock, 1897) = foramen pro ramo nervi vidiani
foramen occipitale (Siebenrock, 1897) = foramen magnum
foramen occipitale magnum (Ogushi, 1911) = foramen magnum
foramen ovale (Kesteven, 1910) = foramen nervi trigemini
foramen ovale (Ogushi, 1911) = fenestra ovalis
foramen palatino-nasale (Siebenrock, 1897) = foramen orbito-nasale
foramen perilymphaticum (Nick, 1912) = fenestra perilymphatica
foramen posterior canalis carotici (Ogushi, 1911) = foramen posterior canalis carotici interni
foramen pro nervo glossopharyngeo (Siebenrock, 1897) = foramen internum nervi glossopharyngei
foramen pro nervo hypoglosso (Ogushi, 1911) = foramen nervi hypoglossi
foramen sphenoidale (Siebenrock, 1897; Ogushi, 1911; Nick, 1912) = foramen nervi trigemini
foramen temporale (Kesteven, 1910) = foramen stapedio-temporale
foramen vago-accessorium (Kesteven, 1910) = foramen jugulare anterius
foramen vestibuli (Siebenrock, 1897) = fenestra ovalis
fossa hypophyseos (Siebenrock, 1897; Nick, 1912) = sella turcica
fossa jugularis (Ogushi, 1911) = cavum acustico-jugulare (in part)
fovea articularis (Siebenrock, 1897) = area articularis mandibularis

fovea major (Nick, 1912) = recessus labyrinthicus proöticus
goniale (Nick, 1912) = os praearticulare
hiatus posterior canalis carotici (Kesteven, 1910) = foramen posterior canalis carotici interni
incisura columellae (Siebenrock, 1897) = incisura columellae auris
incisura ductus cochlearis (Ogushi, 1911) = foramen aquaducti vestibuli
incisura jugularis posterior (Siebenrock, 1897; Nick, 1912) = foramen jugulare posterius
intermaxillare (Ogushi, 1911; Nick, 1912) = os praemaxillare
lamina alisphenoidea (Kesteven, 1910) = processus inferior parietalis
meatus auditorius (Siebenrock, 1897) = fossa acustico-facialis
meatus auditorius internus (Ogushi, 1911) = fossa acustico-facialis
operculare (Siebenrock, 1897; Ogushi, 1911) = os praearticulare
operculare (Nick, 1912) = os spleniale
os occipitale basilare (Kesteven, 1910) = os basioccipitale
os occipitale laterale (Kesteven, 1910) = os exoccipitale
os occipitale superius (Kesteven, 1910) = os supraoccipitale
os postfrontale (Kesteven, 1910) = os postorbitale
ostium superius canalis inframaxillaris (Ogushi, 1911) = fossa meckelii
otosphenoideum (Siebenrock, 1897) = os proöticum
paraquadratum (Siebenrock, 1897) = os quadrato-jugale
paraoccipitale (Siebenrock, 1897) = os opisthoticum
pars sellae (Kesteven, 1910) = sella turcica
pediculus ossis quadrati (Kesteven, 1910) = processus epipterygoideus
pleuroccipitale (Siebenrock, 1897) = os exoccipitale
postfrontale (Siebenrock, 1897; Ogushi, 1911; Nick, 1912) = os postorbitale
praeoperculare (Siebenrock, 1897) = os spleniale
processus clinoideus anterior (Ogushi, 1911) = rostrum basisphenoidale
processus clinoideus posterior (Ogushi, 1911) = processus clinoideus
processus condyloideus occipitalis (Ogushi, 1911) = condylus occipitalis
processus ectopterygoideus (Siebenrock, 1897; Nick, 1912) = processus pterygoideus externus
processus epipterygoideus (Kesteven, 1910) = crista pterygoidea
processus labyrinthicus (Ogushi, 1911) = processus interfenestralis
processus paroccipitalis (Kesteven, 1910) = tuberculum basioccipitale
processus posterior basioccipitalis (Ogushi, 1911) = tuberculum basioccipitale
processus pterygoideus (Nick, 1912) = processus epipterygoideus
processus trabeculae inferiores (Siebenrock, 1897) = rostrum basisphenoidale
ramus suspensorius (Kesteven, 1910) = processus articularis
recessus ampullae posterioris (Nick, 1912) = recessus labyrinthicus opisthoticus
recessus cavum tympani (Siebenrock, 1897) = cavum acustico-jugulare
recessus posterior ampullaris (Ogushi, 1911) = recessus labyrinthicus opisthoticus
recessus pro sinu superiore utriculi (Nick, 1912) = recessus labyrinthicus supraoccipitalis
recessus superior (Ogushi, 1911) = recessus labyrinthicus supraoccipitalis
recessus vestibularis anterior (Ogushi, 1911) = recessus labyrinthicus proöticus
recessus vestibularis opisthoticus (Kesteven, 1910) = recessus labyrinthicus opisthoticus

recessus vestibularis proöticus (Kesteven, 1910) = recessus labyrinthicus proöticus
rima nasalis (Ogushi, 1911) = fissura ethmoidalis
rostrum ossis basisphenoidei (Kesteven, 1910) = rostrum basisphenoidale
sinus mastoideus (Ogushi, 1911) = antrum postoticum
sulcus columellae auris (Kesteven, 1910) = incisura columellae auris
sulcus ethmoidalis (Kesteven, 1910) = sulcus vomeri
sulcus inframaxillaris (Ogushi, 1911) = sulcus cartilaginis meckelii
sulcus jugularis (Kesteven, 1910) = sulcus cavernosus
sulcus pro nervo vago et accessorio (Ogushi, 1911) = foramen jugulare posterius
sulcus vestibularis epioticus (Kesteven, 1910) = recessus labyrinthicus supraoccipitalis
supraangulare (Siebenrock, 1897; Nick, 1912) = os surangulare
suprangulare (Ogushi, 1911) = os surangulare
trabeculae (Nick, 1912) = rostrum basisphenoidale
trochlea proötica (Ogushi, 1911) = processus trochlearis
tuberculum ovoideum (Kesteven, 1910) = crista dorsalis basioccipitalis
vestibulum (Siebenrock, 1897; Nick, 1912) = cavum labyrinthicum

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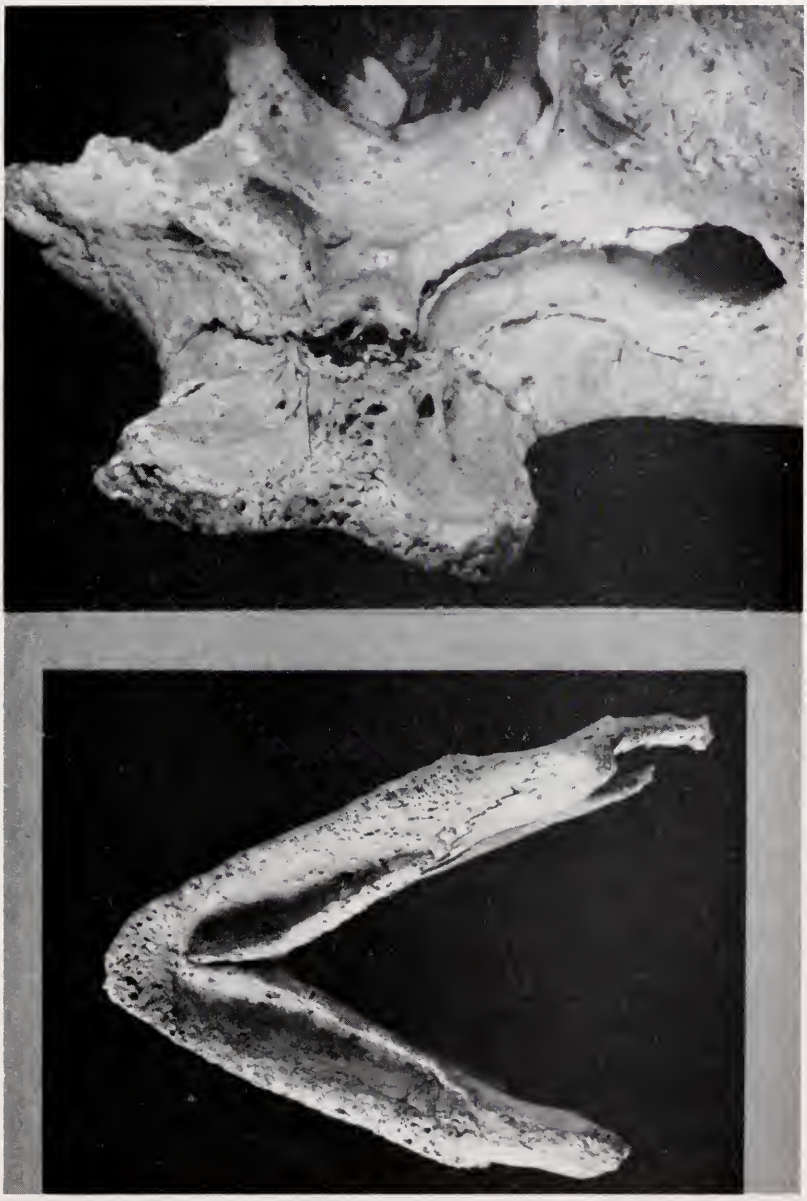
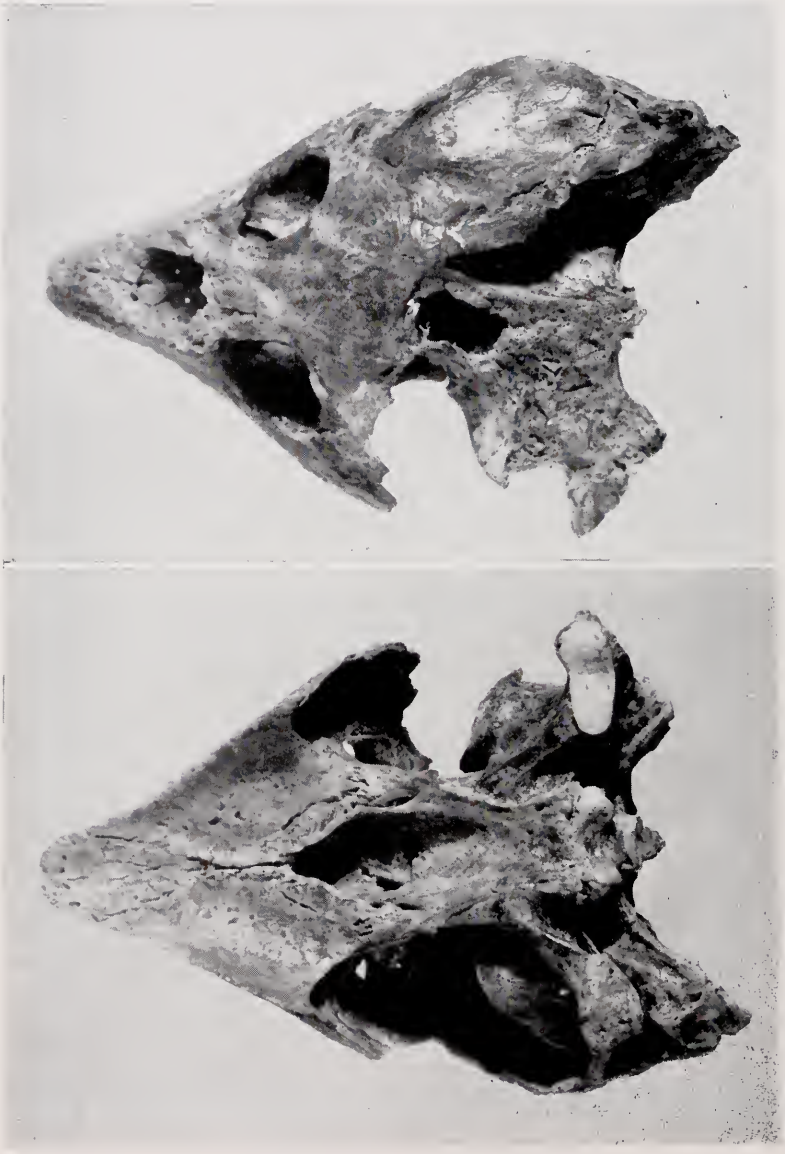
PLATES

1. Portland skull. British Museum R2914. Palatal view.
(Courtesy of the British Museum)

2. Portland skull. British Museum R2914. Left lateral view.
(Courtesy of the British Museum)



3. Upper: Portland skull. British Museum R3163. Anterior view of skull fragment. (See Text-fig. 8).
Lower: Portland mandible. British Museum R2914. Dorsal view.
(Courtesy of the British Museum)



4. Solenhofen skull. Teyler Museum.
Upper: dorsal view. Lower: palatal view.

5. *Proganochelys quenstedti*, Stuttgart skull. Upper: lateral view. Lower: palatal view.

(Courtesy of the Stuttgart Museum)

6. *Proganochelys quenstedti,* Stuttgart skull. Upper: anterior view. Lower: posterior view.

(Courtesy of the Stuttgart Museum)

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 125 No. 4

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By J. M. Gallardo

Museo Argentino de Ciencias Naturales, Buenos Aires.

With One Plate

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No. 4 — *On the Species of Pseudidae (Amphibia, Anura)*

By J. M. Gallardo

INTRODUCTION

A very substantial contribution towards an understanding of the systematics of the frogs of the genera *Pseudis* and *Lysapsus* was achieved by Savage and Carvalho (1953). A few points, however, appear to require modification, among them the status of *Pseudis mantidactylus* Cope (thought by Savage and Carvalho to be a synonym of *P. paradoxus*).

A preliminary examination of specimens of *Pseudis mantidactylus* in the collection of the Sección Herpetología del Museo Argentino de Ciencias Naturales, of the Facultad de Ciencias Exactas y Naturales de la Universidad de Buenos Aires and of the Colegio Nacional de Buenos Aires (Argentina), as well as of others collected by myself in Argentina, Provincia de Buenos Aires (Paso de la Noria, San Miguel, Bella Vista, Santo Domingo), impressed upon me the constancy of the shape and position of the dark and light bands of the ventral aspect of the thighs. In contrast, specimens of *Pseudis paradoxus* from Rosario, Santa Fé and Corrientes, showed a quite different thigh pattern. The specimens of *P. paradoxus* from other areas in the Museum of Comparative Zoology (MCZ), United States National Museum (USNM), the American Museum of Natural History (AMNH), Chicago Natural History Museum (CNHM), and Carnegie Museum (CM) collections, which I was able to examine in 1959-60, showed still other patterns of thigh coloration. Such facts as these led me to regard *P. mantidactylus* as a distinct species and to recognize several subspecies within *P. paradoxus* as well. A study of *Lysapsus limellus* showed the existence of races in this form also.

My previous studies on *Bufo granulosus* and its subspecies have convinced me that there has been recognition of too many species and subspecies without proper reference to the ecological and physiographical features of the environment. I have attempted to study the present species in relation to natural geographical units, such as the hydrographical systems of South America. Such a procedure is particularly useful for the Pseudidae, which are exceedingly aquatic. The species I know best is *P. mantidactylus*. I am familiar with it in the wild and I have never seen it come out of the water voluntarily; instead, it stays always in pools and slow creeks, covered with floating vegetation (*Lemna* sp. and *Jussiaea* sp.). Fernández and Fernández (1921:

139) also report that *P. mantidactylus* in captivity does not leave the water, remaining in small muddy puddles. Possibly individuals move from pool to pool following heavy rains; ordinarily, however, the several populations very definitely tend to remain each within a given hydrographical basin. This is very apparent in the distributional patterns; of the six subspecies of *Pseudis paradoxus* which I describe below, one is restricted to the Guianas, another to the Orinoco system, others to the São Francisco, Arassuahy and Beni rivers and a last one to the Río de la Plata basin. It is not improbable that further subspecies may be recognized in the intervening regions.

PSEUDIS PARADOXUS (LINNAEUS)

Description of the species as a whole. Snout more or less sharp, canthus rostralis indistinct. Loreal region oblique. Tympanum distinct. Vomerine teeth between the choanae large, forming two straight bars, little separated. Tongue rounded, with a small notch. Male with a single internal vocal sac. Small granulations on the dorsum, extending on to the hind limbs. In the pectoral region two sharp angular marks, corresponding to the scars produced in metamorphosis by the eruption of the fore limbs (a character persistent in the adult). Fore limbs relatively weak; fingers long, the pollex opposable; all fingers with cutaneous fringes, and with basal interdigital membranes between the second, third and fourth fingers; a long internal palmar tubercle and a small external one; simple subarticular tubercles. Proximal part of the arm wholly included in skin of body. Hind limbs strong, thigh and leg broad. Tarsal fold present; internal metatarsal tubercle more or less developed (varying according to subspecies); no external metatarsal tubercle, cutaneous fringe on the outermost and innermost toes; interdigital membrane well developed, inserting between the metatarsals and extending to the terminal half of the dilatations; subarticular tubercles simple. Dorsal coloration intermediate between greenish and brown, with darker spots. Venter with more or less abundant brown spotting. Four longitudinal dark lines and alternate light spaces in the ventral aspect of the thigh (the shape and disposition of these dark lines vary in the different subspecies; in the descriptions I shall number them from 1 to 4, starting from the external edge). A long light spot over the cloaca and one or two below it, prolonged by a row of light spots.

Skeletal characters. Skull with swollen otic region; occipital condyles widely separated. Correlated with this, the atlas with two anterolateral prominences to receive the condyles which are far apart, the space between the prominences concave (i.e. "odontoid process" absent). [A similar atlas exists in some Leptodactylidae (*Leptodactylus, Eleutherodactylus*), Hylidae (*Hyla*), some Ranidae (*Arthroleptides, Ocidozyga*) and Phrynomeridae

Fig. 1. Atlas and occiput of *Bufo spinulosus* (left) compared with atlas and occiput of *Pseudis paradoxus* (right).

(*Phrynomerus*). In other Leptodactylidae (*Batrachophrynus, Telmatobius, Ceratophrys, Calyptocephala*), Pelobatidae (*Scaphiopus*), Pelodytidae (*Pelodytes*), some Ranidae (*Astylosternus, Rana*) and Bufonidae (*Bufo*), there are no lateral prominences; instead the median portion of the articular surface is convex (i.e. "odontoid process" present) and the occipital condyles are closer to each other. This characteristic of the *Pseudis* atlas makes it inadvisable to group *Batrachophrynus, Telmatobius, Ceratophrys* and *Calyptocephala* with *Pseudis* in a subfamily Pseudinae as Noble suggested. In addition, however, the presence of an accessory phalanx in all digits excludes from the Pseudinae not only the genera just mentioned but also other genera such as *Eleutherodactylus* which Noble also wished to place in the subfamily, and which do show the *Pseudis* type of atlas.] Transverse processes of the vertebrae, including the second and sacral, approximately cylindrical; at the proximal end of the urostyle there is a neural arch as in a 10th vertebra (cf. some skeletons of *Batrachophrynus macrosternum*); close to this there is a 10th pair of the calcarean sacs. Pectoral girdle arciferal, omosternum plus a xiphisternum as a short, notched, cartilaginous plate. Terminal phalanges long, reaching the tips of the digits, i.e. discs not present.

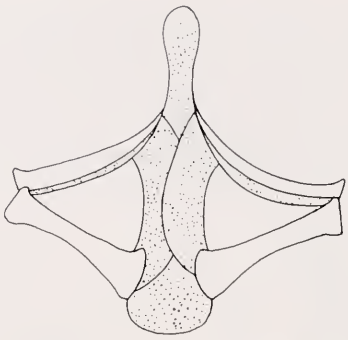

Fig. 2. Pectoral girdle of *Lysapsus mantidactylus*.

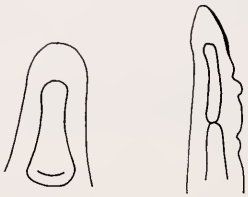

Fig. 3. Outline of tip of toe in relation to terminal phalanx. *Lysapsus mantidactylus*, left, dorsal view; right, lateral view.

SUBSPECIES OF PSEUDIS PARADOXUS

To differentiate the subspecies of *Pseudis paradoxus*, I use the following morphological characteristics: size of vomerine teeth, size of tympanum, whether the supratympanic fold is more or less visible, the shape of the internal metatarsal tubercle; and the following color characters: number of dark bands on the back, ventral spots on throat, breast and abdomen, dark lines and light spaces on the ventral thigh, one or two light spots below cloaca, and coloration of the ventral tibia.

Pseudis paradoxus paradoxus (L.)

1758 *Rana paradoxa* Linnaeus, p. 212.
1830 *Pseudis paradoxa* Wagler, p. 203; Günther, 1858, p. 5; Boulenger, 1882, p. 186.

Description. Adult male MCZ 12136, Demerara, British Guiana. The longitudinal diameter of the tympanum is equal to

eye diameter and also to the distance from eye to nostril. Supratympanic fold not distinct. Vomerine teeth large, with little separation. Metatarsal tubercle conical, oblique, not hooked. Back with four longitudinal dark lines, more or less interrupted. Dark spots on the dorsal aspect of limbs — longitudinal on the anterior limbs and transverse or oblique on the posterior limbs; external edge of the tibia with a dark longitudinal line; internal edge of tarsus dark. Dark spots on the interdigital membrane. Brown irregular spots on the throat and the ventral aspect of the fore limbs. On the pectoral region a dark comma-shaped line on each side at the pectoral angular scars; another pair of more lateral spots. Abdomen with scattered small round spots. Ventral surface of the thigh with longitudinal dark lines not very wide, sometimes broken up and with angular projections; the space between line 1 and the external edge is light and with irregular long spots; space between lines 1 and 2, light, immaculate, without invading angular projections from the bounding lines; space between 2 and 3 with such angular projections; lines 3 and 4 frequently joined towards the middle of the femur; space between line 4 and internal edge with angular projections that form light rectangles. Two light long spots below the cloaca. Ventral aspect of tibia with abundant short irregular lines.

Dimensions: Head and body 56 mm. Head length 18 mm. Head width 19 mm. Head height 8 mm. Eye 6 mm. Interorbital space 6 mm. Elbow to third finger 30 mm. Femur length 30 mm. Tibia length 32 mm. Tibia width 11 mm. Heel to fourth toe 45 mm. Foot length 32 mm. Adult female, same origin, MCZ 12135, head and body 54 mm.

Distribution: This subspecies is restricted to the British and Dutch Guianas.

Material studied: MCZ 12135-6 (2 specimens) British Guiana, Demerara, coast lands, E. Smith; MCZ 2775 (1 specimen) British Guiana, Demerara, C. W. Beebe, 1909; AMNH 13566-8 (3 specimens) British Guiana, Demerara River, Alayma, J. Rodway; MCZ 3901-2 (2 specimens) British Guiana, trenches near Georgetown, J. Rodway, 1914; AMNH 1305 (1 specimen) British Guiana, J. Rodway, 1912; AMNH 21423, 39588, 39638-40 (5 specimens) British Guiana, Georgetown; AMNH 49259 (1 specimen) British Guiana, Essequibo River, R. Snediger, V-31-1937; AMNH 5103 (1 specimen) Dutch Guiana, Paramaribo, J. A. Samuels; AMNH 24013 (1 specimen) Guiana.

PSEUDIS PARADOXUS CARIBENSIS subsp. nov.

1933 *Pseudis paradoxa* Parker, p. 10; 1934, p. 123; Gans, 1956, p. 2 (part); Kenny, 1956, p. 23.
1942 *Pseudis paradoxis* Ditmars, p. 51.
For diagnostic features see Table 1.

Description. Type, adult female MCZ 19890, Mayaro Bay, Trinidad, B. W. I. Tympanum rather smaller than the eye and smaller than the distance between eye and nostril. Oblique fold above the tympanum indistinct, but marked by a dark line. Vomerine teeth large, with little separation. Metatarsal tubercle with narrow base, forming a small hook. Back with six longitudinal dark lines more or less discontinuous. Dorsal surface of limbs and interdigital membrane as in the preceding subspecies. Throat, pectoral and abdominal regions with dark rounded spots (more abundant on the throat and breast). Ventral surface of thigh with thinner lines than in *P. p. paradoxus;* space between line 1 and external edge, with elongated punctations and spots; space between lines 1 and 2 light; space between lines 2 and 3 with abundant elongate spots; space between 3 and 4 light (the fourth line wider); between line 4 and internal edge abundant, elongate, irregular spots. One light, long, spot below the cloaca. Tibia ventrally with abundant short, irregular, lines. (The ventral coloration of the hind limbs is also perfectly visible in four-legged tadpoles.)

Dimensions: Head and body 64 mm. Head length 22 mm. Head width 25 mm. Head height 11 mm. Eye 6 mm. Snout height 4 mm. Interorbital space 7 mm. Elbow to third finger 33 mm. Femur length 39 mm. Tibia length 33 mm. Tibia width 11 mm. Heel to fourth toe 50 mm. Foot 36 mm. *Paratype*, adult male, CM 33787, head and body 60 mm.

Distribution: Nearly all the material that has been studied by me comes from the same locality, Mayaro, S.E. Trinidad Island. (This locality has recently been described, and photographs of it published by Gans, 1956.) Additional Trinidad localities have been reported by Kenny (1956): Plum Mitan ricefields near Biche (tadpoles); Icacos swamp near Cedros (adults); Apex oilfields at Fyzabad (males singing). This subspecies, however, seems to exist also in Venezuela. At least the specimen of *Pseudis paradoxus* figured by Lutz (1927, Plate II, figs. 18-19), from Maracay, Venezuela, has a ventral pattern similar to the Trinidad specimens. I have seen also one specimen from Hato Gabinero, Venezuela, that in general has the characteristics of this subspecies. In

this specimen the ventral coloration of the thighs is nearly the same as typical *P. p. caribensis*, with spots in the space between line 1 and external edge; some spots (but few and small) in the distal portion of the space between 2 and 3; short and irregular lines between the knee and the union of 3 and 4; moreover the comma-shaped spots on the pectoral region are lacking and the metatarsal tubercle is hook shaped. Other characteristics are close to those of *P. p. paradoxus*, as is the presence of four interrupted longitudinal dark dorsal bands; it is, however, different from both subspecies by having the ventral surface of the tibia without spots.

Material studied: MCZ 19890-1; 19893 (3 specimens) Trinidad, Mayaro Bay, N. A. Weber, XII-1934; MCZ 19892 (1 skeleton) Trinidad, Mayaro Bay; MCZ 26157 (1 specimen) Trinidad, St. Bernard Estate, Mayaro, M. G. Kugler, 1945; CNHM 49705-6 (2 specimens) Trinidad, Plaisance Mayaro, Stander, 1947; CM 33787 (1 specimen) Trinidad, Pond at Mayaro, C. Gans, IX-22-1953; USNM 137347 (1 specimen) Venezuela, Cojedes, Hato Gabinero near San Carlos, Pérez, IV-8-1955.

Pseudis paradoxus bolbodactylus A. Lutz

1925 *Pseudis bolbodactyla* A. Lutz, p. 138; Cochran, 1955, p. 312, fig. 20, Pl. 32, figs. G, H.

Description. Female, MCZ 25729, Lagoa do Curralinho, Lassance, Minas Gerais, Brasil. Tympanum rather smaller than the eye and smaller than the distance from eye to nostril. Supratympanic fold not very evident. Vomerine teeth more reduced than in the two preceding subspecies and separated on the mid line. Metatarsal tubercle more or less conical, not forming a hook. An interocular spot produced posteriorly on the two sides in two broad arms with an indentation between, thence continued on the back by two longitudinal irregular lines. Dorsal aspect of limbs with spots, internal edge of the femur with large light-edged ocelli. Interdigital membrane of the foot with spots barely evident. Throat, pectoral and abdominal regions with dark rounded spots, more abundant on the breast. Ventral region of thigh with relatively thick lines, but several of them interrupted, space between line 1 (which is rather curved) and the external edge light; proximally between lines 1 and 2 an elongate spot (line 2 starts with two spots); space between lines 2 and 3 light (line 3 composed of elongate spots); space between 3 and 4 light (line 4 is formed by round spots); space between 4 and internal edge light. One light long spot below the cloaca. Ventral aspect of tibia with a few dark spots.

Dimensions: Head and body 45 mm. Head length 16 mm. Head width 17 mm. Head height 8 mm. Eye 4 mm. Interorbital space 3 mm. Elbow to third finger 22 mm. Femur length 25 mm. Tibia length 24 mm. Tibia width 9 mm. Heel to fourth toe 35 mm. Foot 27 mm.

Variation: In general the lines on the thigh are not so much interrupted as in the specimen described, especially lines 3 and 4, which are usually continuous or have one spot at the beginning or at the end. More constant is the short line in the space between 1 and 2 (sometimes united to line 2 and forming an angle) and the spot at the beginning of line 2. This subspecies has many similarities with *P. p. platensis*, but it is different in having line 1 thinner, no angular projections from any of the lines and no fusion of lines 3 and 4.

Distribution: Confined to the São Francisco River in the State of Minas Gerais, Brasil. Cochran (1955: 215) cites material from various localities in this state and from Itá in the state of Espirito Santo, though it would be interesting to check whether the present subspecies or another one exists in the latter locality.

Material studied: MCZ 25729 (1 specimen) Brasil, Minas Gerais, Lassance, Lagoa do Curralinho, Cochran and Venancio; USNM 98534 (1 specimen) Brasil, Piraporá, III-23-1935; USNM 98173, 175-79, 181-88, 190-95, 197-99, 200, 202 (25 specimens) Brasil, Lassance, Lagoa do Curralinho, Cochran and Venancio, III-22-1935; USNM 97022 (1 cotype) Brasil, Minas Gerais, Lassance, Lagoa de Genipapo.

Pseudis paradoxus fuscus Garman

1883 *Pseudis fusca* Garman, p. 47; Cochran, 1955, p. 216, Pl. 32, figs. I-K.

Description. Cotype MCZ 1872, Rio Arassuahy, Minas Gerais, Brasil. Tympanum approximately the same size as the eye and as the distance from eye to nostril. Supratympanic fold present. Snout relatively short (a variable character in *P. p. paradoxus*). Vomerine teeth relatively reduced and separated in the middle. The metatarsal tubercle not forming a hook. Dorsal color pattern rather indistinct; ground color of cotype brown, perhaps due to poor preservation; ventral parts light, rather spotted towards the throat. In the cotype it is practically impossible to see the coloration of the ventral aspect of the femur, though it would seem that the space between line 1 and the external edge has abundant dark

spots. Space between line 4 and the internal edge, with large irregular light spots. A light line above the cloaca; another light line below it, nearly divided into two spots and continued by other light spots. Ventral aspect of tibia with abundant irregular dark spots.

Fig. 4: Ventral aspects of thighs in *Pseudis* and *Lysapsus*. Upper row: left, *P. p. paradoxus* MCZ 12135; center, *P. p. caribensis* MCZ 19890; right, *P. p. bolbodactylus* MCZ 25729. Lower row: left, *P. p. platensis* MCZ 24808; center, *P. p. occidentalis* MCZ 29961; right, *Lysapsus mantidactylus* MCZ 28730.

Dimensions: Head and body 51 mm. Head length 16 mm. Head width 19 mm. Head height 8 mm. Eye 6 mm. Interorbital space 4 mm. Elbow to third finger 26 mm. Femur 29 mm. Tibia length 28 mm. Tibia width 9 mm. Heel to fourth toe 36 mm. Foot 26 mm. Another cotype, head and body 41 mm.

Distribution: No specimens have been reported since Garman's, and the only known locality is the Arassuahy River in the State of Minas Gerais. This locality is very close to that of *P. p. bolbodactylus*, but separated by the Serra do Espinhaço which divides the São Francisco basin from that of the Jequitinhonha

basin, to which the Arassuahy River belongs. Partly on the basis of this geographical separation (cf. Cochran 1955: 217) and in spite of the absence of new material, I am disposed to retain this form as distinct from *P. p. bolbodactylus*.

Material studied: MCZ 1872 (2 specimens) cotypes, Brasil, Minas Gerais, Rio Arassuahy, Hartt and Copeland, Thayer Expedition, 1864-7.

Pseudis paradoxus platensis subsp. nov.

1894 *Pseudis paradoxa* Boulenger, p. 347; Miranda Ribeiro, 1926, pl. 11, figs. 1-1a; Müller and Hellmich, 1936, p. 27, fig. 9; Freiberg, 1942, p. 228 (part); Travassos and Freitas, 1942, p. 284; Vellard, 1948, p. 173; Cei, 1956, pl. V, figs. 36-37; Gans, 1960, p. 303 (part).

For diagnostic features see Table 1.

Description. *Type*, adult male, MCZ 24808, Colonia Nueva Italia, Dept. Villeta, Paraguay. Tympanum approximately the same size as the eye and as the distance from eye to nostril. Practically no supratympanic fold. Vomerine teeth large, with little separation. Metatarsal tubercle rather prominent, but without hook. On the back two large dark spots shaped like commas, extending from the interorbital space to the scapular region; two interrupted dorsal dark lines. Dorsal aspect of the limbs and interdigital membrane of the foot with dark spots. Throat, pectoral and abdominal regions with more or fewer round dark spots. Ventral aspect of the thigh with dark thick lines; space between line 1 and external edge without spots; space between line 1 and line 2 with an extensive proximal spot; light space between line 2 and line 3 with the projections from the lines only slightly indicated; space between line 3 and line 4 light; between line 4 and the internal edge, light rectangles. Two light long spots below the cloaca. Ventral aspect of tibia with extended dark spots interrupted and irregular.

Dimensions: Head and body 50 mm. Head length 15 mm. Head width 16 mm. Head height 7 mm. Eye 5 mm. Interorbital space 3 mm. Elbow to third finger 24 mm. Femur length 28 mm. Tibia length 25 mm. Tibia width 8 mm. Heel to fourth toe 36 mm. Foot 25 mm. *Paratype* MCZ 24809, from the same locality, head and body 42 mm.

Distribution: This subspecies is found from the Upper Paraguay River to Rosario (Santa Fé) on the banks of the Paraná

Table 1: The diagnostic features of the subspecies of Pseudis paradoxus

	paradoxus	caribensis	bolbodactylus	fuscus	platensis	occidentalis
Vomerine teeth	Large	Large	Medium size	Medium size	Large	Large
Tympanum - eye/ eye - nostril	Same size	Smaller	Smaller	Same size	Same size	Smaller
Supratympanic fold	Not distinct	Not distinct, but with dark line	Not distinct	Present	Not distinct	Covers part of tympanic membrane
Metatarsal tubercle	Not hooked	Hooked	Not hooked	Not hooked	Not hooked	Not hooked
Ventral coloration of thigh	Dark lines not very wide. Space 1-ext. long spots; 2-3, 4-int. angular projections; 1-2, 3-4 without spots	Dark lines thinner. Space 1-ext., 2-3, 4-int. long spots; 1-2, 3-4 without spots	Dark lines wide. Spaces without spots, except 1-2 which has a long basal spot	Spots 1-external edge	Dark lines wide. Space 1-2 a long spot, 4-int. light rectangles; others without spots	Dark lines very blurred, sometimes 1 and 2 missing. Spaces without spots
Longitudinal dorsal lines	Four	Six	Two	----	Two	Four
Ventral tibia	Abundant short dark lines	Short dark lines	Some long dark spots	Abundant long dark spots	Some long dark spots	Without spots
Ventral body	Spots: throat, breast (comma-shaped), abdomen (scarce)	Round spots. More abundant in throat and breast	More abundant on throat	Throat spotted	Round spots	Without spots
Light spots below cloaca	Two	One	One	----	Two	One

River. In Brasil it has been collected in Mato Grosso: S. Luiz de Cáceres (the northernmost locality known at present) and near Bodoquena; in Bolivia, San Fermín at 100 km NW of Puerto Suárez and in nearby El Carmen; in Paraguay, near Asunción, Fortín Esteros and Nueva Italia; in Argentina in the Provinces of Misiones, Corrientes (Ituzaingó, Isla Apipé) and Santa Fé (La Geraldina, Santa Fé, Rosario).

Material studied: MCZ 24808-9 (2 specimens) Paraguay, Dept. Villeta, Colonia Nueva Italia, P. Willim, XII-6-1943; CNHM 42313-4 (2 specimens) Paraguay, Colonia Nueva Italia, P. Willim; AMNH 50657 (1 specimen) Paraguay, Villeta, Colonia Nueva Italia, P. Willim; MCZ 29958 (1 specimen) Bolivia, El Carmen, C. Gans, II-26-1954.

Pseudis paradoxus occidentalis subsp. nov.

1956 *Pseudis paradoxa* Gans, p. 2 (part); Gans, 1960, p. 303 (part).

For diagnostic features see Table 1.

Description. Type, adult male, MCZ 29961, El Pailón, Bolivia. Tympanum slightly smaller than the eye and smaller than the distance from eye to nostril. The skin of the supratympanic fold covers part of the tympanic membrane. Loreal region slightly concave. Vomerine teeth large, very slightly separated. Metatarsal tubercle rather prominent, but without hook. Back brown with four black longitudinal lines which are very irregular and have lateral projections, forming dark edged circles towards the rear. Dorsal aspect of the extremities with dark spots. Internal edge of the tarsus dark. Interdigital membrane of the foot with large dark spots. Sides of trunk with light spots. Ventral aspect of thigh with the four dark lines very blurred (sometimes lines 1 and 2 are missing); lines 3 and 4 are more distinct and thicker; the spaces among the lines are light. One light long spot below the cloaca. The fourth ventral line of thigh follows the internal edge. Tibia ventrally light. Throat, pectoral and abdominal regions light and unspotted (in the male the throat slightly darker).

Dimensions: Head and body 51 mm. Head length 18 mm. Head width 20 mm. Head height 9 mm. Eye 5 mm. Interorbital space 6 mm. Elbow to third finger 23 mm. Femur 25 mm. Tibia length 26 mm. Tibia width 9 mm. Heel to fourth toe 35 mm. Foot 27 mm. *Paratype* MCZ 29959, adult female, the same locality, head and body 72 mm.

Distribution: Though the material studied, with good locality, comes from only one place in Bolivia, El Pailón, it is possible that this susbspecies occupies the valleys of the Beni and its tributaries. Recently, Shreve (1959) has described a new species of *Phyllomedusa* (*P. pailona*) from the same locality, remarking that *Phyllomedusa sauvagii*, its closest relative, was collected by Gans in El Carmen: this distribution parallels that of *Pseudis paradoxus occidentalis* and *P. p. platensis*.

Material studied: MCZ 29959, 61 (2 specimens) Bolivia, El Pailón, C. Gans, III-5-1954; USNM 94390 (1 specimen) South America, J. H. Lunn, 1932.

INTERRELATIONSHIPS OF THE SUBSPECIES

P. p. paradoxus, *P. p. caribensis* and *P. p. occidentalis* of northern and western South America seem to me more closely related, while *P. p. fuscus* and *P. p. bolbodactylus* of southeast Brasil form another group. *P. p. platensis* provides the connecting link.

THE STATUS AND ALLOCATION OF PSEUDIS MANTIDACTYLA COPE

This species must be considered distinct from *Pseudis paradoxus* and more closely related to *Lysapsus limellus*. In general it fits the definition of the genus *Lysapsus* given by Savage and Carvalho (1953: 194). Thus it has terminal discs on the digits, the interdigital webbing of the toes reaching to the base of the discs; the vomerine teeth arranged obliquely, slightly towards the rear of the choanae; the pectoral girdle with a long and cartilaginous omosternum, of the same length as the epicoracoids. It differs specifically from *L. limellus* in having the terminal phalanx of the toes relatively not so short, although they do not reach the extreme end of the digits on account of the presence of discs and in the male with two vocal sacs. (The latter character also separates *mantidactylus* from *paradoxus*.)

I propose therefore that Cope's species be called *Lysapsus mantidactylus* (Cope). Parentheses are used since the generic name employed by Cope (1862b: 352) in the original description was *Pseudis* and not *Lysapsus*, as wrongly stated by Boulenger (1882: 187), Freiberg (1942: 228), Savage and Carvalho (1953: 193) and Cei (1956: 57).

Lysapsus mantidactylus (Cope)

1862b *Pseudis mantidactyla* Cope, p. 352; Boulenger, 1882, p. 187, 1883, p. 17; Boettger, 1892, p. 26; Berg, 1896, p. 162; Fernández and Fernández, 1921, p. 134; pl. III, figs. 14-15; Nieden, 1923, p. 367; Miranda Ribeiro, 1926, p. 25; Freiberg, 1942, p. 228; Gallardo, 1957, p. 354, 1958, pp. 291-298.

1953 *Pseudis paradoxus* Savage and Carvalho, p. 193 (part); Cei, 1956, p. 57 (part).

Description. Adult female, MCZ 25730, Uruguay, Montevideo. Tympanum equal to eye diameter and slightly larger than the distance from eye to nostril. Head relatively shorter than in *P. paradoxus;* practically no canthus rostralis. Vomerine teeth short and separated, placed slightly to the rear of the choanae. Small granulations on dorsum and hind limbs, forming lines on the tibia. Leg (tibial region) thinner than in *P. paradoxus.* The interdigital membrane only at the base of the fingers prolonged onto the toes by digital fringes which reach the base of the terminal discs. The metatarsal tubercle sharp and oblique, not forming a hook. Tarsal fold not very prominent. One light oblique band from the eye to the corner of the mouth. Back with some dark spots. Sides of the trunk with a light longitudinal band. A longitudinal dark band on the side of the fore limb. Throat with some scattered spots, pectoral and abdominal regions light. Ventral design of the femur: dark longitudinal lines, better defined, in increasing order 1, 2, 3, 4; line 1 very blurred, formed of long irregular spots; spaces among the lines light. One light band over the cloaca and a fifth dark band at the level of the cloaca; space between dark lines 4 and 5, light. Tibia ventrally with infrequent spotting, more abundant on the edges.

Skeletal characters: Skeleton bluish green (in live animals and freshly preserved specimens); Boulenger (1883: 17) makes reference to this coloration. A green skeleton is also found in other species of the genus, as in *L. limellus* (Miranda Ribeiro, 1926: pl. II, fig. 2a), and according to Parker (1935: 510) in *P. laevis.* Pectoral girdle arciferal; coracoid and precoracoid ossified and well developed; omosternum long and cartilaginous (same length as the epicoracoids); sternum and xiphisternum as a short cartilaginous plate. The terminal phalanges are long, not reaching the tips of the digits.

Dimensions: Head and body 35 mm. Head length 12 mm. Head width 12 mm. Head height 4 mm. Eye 4 mm. Interorbital space 2 mm. Elbow to third finger 18 mm. Femur length 20 mm. Tibia length 19 mm. Tibia width 5 mm. Heel to fourth toe 27 mm. Foot 19 mm.

Distribution: This species, first described by Cope from Buenos Aires, was later reported by Boulenger and also by Boettger from Rio Grande do Sul (Brasil) and Montevideo (Uruguay); by Berg again from Buenos Aires, and Misiones (Argentina); and by Vellard from Salta (Hickman) and Formosa (Puerto Dalmacia) in Argentina. From the material I studied in Argentinian collections and from my own collecting, I can say it is common in the neighborhood of the city of Buenos Aires, extending to the N.E. of the Buenos Aires Province and the lagunas of the Partido de General Lavalle; it can also be recorded for Santa Fé Province, where also exist *Pseudis paradoxus* and *Lysapsus limellus*. Cei (1949: 539) cites it for Corrientes.

Material studied: MCZ 25730 (1 specimen) Uruguay, Montevideo; USNM 71124-6 (3 specimens) Uruguay, Puerto La Paloma, W. L. Smith; USNM 70633-4 (2 specimens) Uruguay, Montevideo; USNM 65617-8 (2 specimens) Uruguay, Montevideo, near Playa Ramirez, H. M. Smith, IX-30-1922; AMNH 11953 (1 specimen) Argentina, Prov. Buenos Aires, Punta Lara, Pedro Serie, VI-15-1920; CNHM 9698 (1 specimen) Argentina, Prov. Buenos Aires, La Plata, K. P. Schmidt, X-28-1926; USNM 22751-2 (2 specimens) Argentina, Prov. Buenos Aires, La Platá; USNM 63506 (1 specimen) Argentina, Prov. Buenos Aires, Dolores, A. Wetmore, X-1920; CNHM 83291 (1 specimen) Brasil, Rio Grande do Sul; CNHM 80554, 60, 90 (3 specimens) Brasil, Rio Grande do Sul, Millstead; MCZ 22996-23000 (10 specimens) Brasil, Rio Grande do Sul, Santa María, L. I. Price and T. E. White, 1936; USNM 118180-1 (2 specimens) Brasil, Rio Grande do Sul, Santa María, L. I. Price and T. E. White, 1936; USNM 121328 (1 specimen) Brasil, Rio Grande do Sul, Santa María, Inst. Butantan.

LYSAPSUS LIMELLUS COPE

Savage and Carvalho (1953: 193) erroneously state that the original description was based on Uruguayan material, when in reality Cope (1862a: 156) says: "Habitat-Paraguay. Taken on ----------river" (leaving blank the name of the river). Though it was first described for Paraguay, Cope later himself (1862b:

351) cites it for Corumbá, Steindachner (1864: 262) for Caiçara, and Miranda Ribeiro, (1926:27) for Cáceres, all three localities in Mato Grosso (Brasil). The latter author reports it also from Rio Grande do Sul (Brasil), Uruguay, and Buenos Aires Province (Argentina). Previously, Boulenger (1889; 246) had reported the species from Resistencia, Chaco, Argentina and (1894: 347) from Asunción, Paraguay; Peracca (1895: 24) added Río Apa, Upper Paraguay, and Berg (1896: 161) Corrientes, Argentina. Müller and Hellmich (1936: 25) and Vellard (1948: 169) had specimens from the Province of Formosa; Santa Fé can be added to the Argentine localities (specimens in the Museo Argentino de Ciencias Naturales). Outside of this general area of the basin of the Paraguay, Paraná, Plata and south of Brasil, Boulenger (1898: 4) lists it for Beni, Bolivia; Baumann (1912: 122, 124, 161) for the Upper Amazon; Müller and Hellmich (1936: 26) for the Marajó Island: Parker (1939:87) for Grão Pará; Savage and Carvalho (1953: 195) for the Pará and Amazonas states. Moreover, Parker (1935: 510) describes a closely related species, *Pseudis laevis*, based on nine specimens from British Guiana and one specimen from the Beni region (Bolivia); Savage and Carvalho (1953: 196) place this species in the genus *Lysapsus*.

In the Museum of Comparative Zoology and in the Chicago Natural History Museum I have studied material from Paraguay and Bolivia, in which some differences are noticeable between specimens from the two localities. These differences permit the species *Lysapsus limellus* to be divided into two subspecies: *L. l. limellus* Cope, from the Paraguay and Paraná basin, and *L. l. boliviianus* subsp. nov. from the Beni Province (Bolivia). I have not seen material from Uruguay nor from southern Brasil; any such specimens belong to the subspecies *L. l. limellus*, but I prefer not to assert this without having seen them. On the other hand, *Lysapsus laevis* can be considered as a third subspecies of *L. limellus*, except for the Beni specimen, which undoubtedly belongs to *L. l. bolivianus*. Finally, it is possible that the specimens from Pará and Amazonas states belong to *L. l. bolivianus;* but specimens from Rio Branco (Brasil) that I saw in the United States National Museum belong to *L. l. laevis*.

Lysapsus limellus limellus Cope

1862a *Lysapsus limellum* Cope, p. 155; 1862b, p. 351.
1882 *Pseudis limellum* Boulenger, p. 187; 1889, p. 246; 1894, p. 347; Boettger, 1885, p. 242; Peracca, 1895, p. 24; Berg, 1896, p. 161; Müller and Hellmich, 1936, p. 25

(part), fig. 8; Vellard, 1948, p. 169.

1953 *Lysapsus limellus* Savage and Carvalho, p. 194 (part).

Description. Adult female, MCZ 25834, Río Pilcomayo, 15 miles W. of Río Paraguay, Chaco, Paraguay. Snout rather sharp, nostrils 2 mm. from the tip of the snout. Back and ventral regions with granulations. Cutaneous fringe of fingers insignificant. Digital discs of the feet elliptic with rather sharp tips. Interdigital membrane not very large; when the toes are adpressed it does not form wide folds.

Coloration: A dark continuous line on the ventral internal edge of the femur; posterior part of the femur without pattern. Small black granulations on the ventral region of the femur.

Dimensions: Head and body 17 mm. Head length 6 mm. Head width 6 mm. Head height 3 mm. Eye 2 mm. Snout 2 mm. Interorbital space 2 mm. Elbow to third finger 10 mm. Femur length 12 mm. Tibia length 12 mm. Tibia width 2 mm. Heel to fourth toe 14 mm. Foot 10 mm.

Distribution: Paraguay and Paraná Rivers and their affluents. From Mato Grosso to Río Tigre (Buenos Aires Province, Argentina), as cited by Miranda Ribeiro (1926: 27). It has been reported in Argentina from Formosa, Chaco, Santa Fé, Corrientes and Buenos Aires. (The photo published by Cei, 1956: pl. V, fig. 38, as of *Pseudis minutus* from Corrientes seems to belong to *L. l. limellus*.)

Material studied: MCZ 25834 (1 specimen) Paraguay, Chaco, 15 miles W. of Río Paraguay, Río Pilcomayo, P. Willim, II-3 to III-3-1944; CNHM 42315-7 (3 specimens) Paraguay, Colonia Nueva Italia, P. Willim, 1944; USNM 139277 (1 specimen) Paraguay, San Bernardo, Lago Ypacaray (beach pools, C. J. D. Brown, VIII-16-1956; USNM 139278 (1 specimen) Paraguay, Asunción Bay, Río Paraguay nr. Asunción, C. J. D. Brown, 1-2-1957; USNM 132739 (1 specimen) Brasil, Mato Grosso, Paraguay River above L. Gahiba-mirim, K. P. Schmidt, 1926; USNM 97146 (1 specimen) Brasil, Mato Grosso, Cáceres; USNM 115975 (1 specimen) Brasil, Mato Grosso, São Luiz de Cáceres, old cut-off of Río Paraguay, V-24-1909; USNM 132992 (1 specimen) Brasil, Mato Grosso, Porto Esperança.

Lysapsus limellus bolivianus subsp. nov.

1898 *Pseudis limellum* Boulenger, p. 4.

1935 *Pseudis laevis* Parker, p. 510 (part).

For diagnostic features see Table 2.

Description. Type, adult male, MCZ 17493, Reyes, Bolivia. Snout shorter than in *L. l. limellus;* nostrils very close to the tip of the snout. Dorsal and ventral skin much granulated. Cutaneous fringe of fingers well devloped. Digital discs of the feet without sharp tips. Interdigital membrane very well developed, forms wide folds when toes adpressed.

Coloration: A continuous dark line on the internal edge of the ventral aspect of the femur, as in *L. l. limellus*, but also another line more external, irregular and interrupted. Hind side of thigh with a third dark line, interrupted, below the cloaca. Less abundant small dark granulations on the ventral aspect of the femur.

Dimensions: Head and body 18 mm. Head length 6 mm. Head width 7 mm. Head height 4 mm. Eye 2 mm. Snout 1.5 mm. Interorbital space 2 mm. Elbow to third finger 9.5 mm. Femur length 12 mm. Tibia length 12 mm. Tibia width 2 mm. Heel to the fourth toe 15 mm. Foot 10 mm. Paratype, adult female, MCZ 10076, from the same locality, head and body 21 mm.

Distribution: The specimens studied come from the NW of Bolivia, Beni Department, Amazonian drainage through the Beni River and the Madeira. Thus it is probable that the specimen which Parker (1935: 510) ascribes to *Pseudis laevis*, from Santa Ana de Movrinas, Beni River, Bolivia, actually belongs to *L. l. bolivianus*. (Boulenger, 1898: 4, reported *L. limellus* from the same locality in Bolivia.) Also very likely to be this subspecies are the specimens of Lower Madeira River in Amazonas State and of Municipio of Monte Alegre in Pará State, Brasil, mentioned by Savage and Carvalho (1953: 195) and considered by them to be *L. limellus* on account of the granulose skin (in contrast to *Pseudis laevis* which has smooth skin).

Material studied: MCZ 10076, 17493 (2 specimens) Bolivia, Reyes, N. E. Pearson; MCZ 10077 (1 specimen) Bolivia, Lake Rogagua, N. E. Pearson.

Lysapsus limellus laevis (Parker)

1935 *Pseudis laevis* Parker, p. 510 (part).

Description. Adult male, USNM 137745, Fraseo, Boa Vista, Rio Branco, Brasil. Snout short. Dorsal and ventral skin smooth. Cutaneous fringe insignificant. Digital discs of the feet nearly round. Interdigital membrane very well developed, forms wide folds when toes adpressed.

Coloration: A continuous dark line on the internal edge of the ventral aspect of the femur; more externally some dark spots in line. A third dark line below the cloaca.

Dimensions: Head and body 21 mm.

Distribution: British Guiana, Rupununi Savannah and Pacaraima foothills; in Brasil, Rio Branco near Boa Vista (this locality is very near the British Guiana boundary).

Material studied: USNM 137744-6 (3 specimens) Brasil, Río Branco, Boa Vista, Fraseo, J. D. Haseman, XII-5-1912.

L. l. limellus and *L. l. laevis* differ in the type of skin, the shape of the snout, the extent of the interdigital membrane and the coloration of the thigh; the two are related by way of *L. l. bolivianus* which has granular skin like *L. l. limellus* but in snout shape, extent of interdigital membrane and in coloration is near *L. l. laevis*, which differs from both by the extent of fringing on the fingers.

L. l. laevis is restricted to the British Guiana and Rio Branco, *L. l. bolivianus* to the Beni drainage and probably also the Amazon, *L. l. limellus* to the system of the Paraguay, Paraná and Plata rivers.

Table 2. Diagnostic features of the subspecies of *Lysapsus limellus*

	limellus	*bolivianus*	*laevis*
Snout	Rather sharp	Obtuse	Obtuse
Nostril from tip of snout	Not very near	Very near	Very near
Dorsal and ventral skin	Granulated	Granulated	Smooth
Cutaneous fringe of fingers	Insignificant	Well developed	Insignificant
Discs of feet	Elliptic with rather sharp tips	Elliptic without sharp tips	Nearly round
Interdigital membrane	Not very large, not forming wide folds	Very well developed, forming wide folds	Very well developed, forming wide folds
Black lines on ventral thigh	Internal edge with a continuous line	Internal edge with a continuous line and a discontinuous line externally	Internal edge with a continuous line and some external spots in line
Posterior side of femur	Without design	With a third line	With a third line

Two of the species of the genus *Pseudis* are difficult to alloeate: these are *P. minutus* Günther, described on a speeimen collected by Darwin from "South America" (later regarded as coming from South Brasil), and *P. meridionalis* Miranda Ribeiro, described from Rio Grande do Sul, Brasil.

Pseudis minutus in some characters approaches *P. paradoxus;* such features are the general shape of the head, the lack of terminal discs and the developmnt of the interdigital membrane; however, it resembles *L. mantidactylus* in size (40 mm. according to Nieden) and in the presence of two vocal sacs (so specified by Günther in the original description, but Boulenger reports only one). If Boulenger was right about the single vocal sac, it is very probable that *P. minutus* is one of the southern races of *P. paradoxus;* we must remember that Cope (1885: 187) reported *P. paradoxus* from Rio Grande do Sul. Doubt was cast on this by Boulenger (1885b: 298) who said confidently that Cope had the species confused with *L. mantidactylus.* I think, however, that this last is not at all probable since *L. mantidactylus* is a species described by Cope.

Pseudis meridionalis, on the basis of its size (20 mm.) and the resemblances to *L. limellus* mentioned by Miranda Ribeiro, could very well be the representative in southern Brasil of the latter species; however, according to Miranda Ribeiro, the digital discs are absent. (It must be remarked that what has sometimes been identified as *P. minutus* or as *P. meridionalis* in many collections is in reality *L. mantidactylus.*) All this makes desirable a better study of the Pseudidae from southern Brasil, based on adequate material.

SUMMARY

1) On the basis of both external and internal characters (pectoral girdle, digital phalanges), *Pseudis mantidactyla* Cope is placed in the genus *Lysapsus.*

2) The color pattern of the ventral aspect of the thigh is sufficiently constant in the species and subspecies of *Pseudis* and *Lysapsus* to be taken as one of the useful characteristics in their classification.

3) The distribution of the subspecies seems to be correlated with the drainage system of the large South American rivers.

4) Six subspecies are defined for *Pseudis paradoxus,* three of them new, and three for *Lysapsus limellus,* one new.

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PLATE

Plate. *Top:* tadpoles of *Lysapsus mantidactylus* (above) and *Pseudis paradoxus* (below). *Bottom:* adults of *Pseudis paradoxus* (left), *Lysapsus limellus* (center), *Lysapsus mantidactylus* (right).

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CORRELATIONS BETWEEN ECOLOGY AND MORPHOLOGY IN ANOLINE LIZARDS FROM HAVANA, CUBA AND SOUTHERN FLORIDA

By Bruce B. Collette

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No. 5 — *Correlations Between Ecology and Morphology in Anoline Lizards from Havana, Cuba and Southern Florida*

By Bruce B. Collette[1]

INTRODUCTION

In many areas of the vast range of the iguanid genus *Anolis* several species occur sympatrically. There is, therefore, very good opportunity to analyze the ecological separation of sympatric species and to test the correlation of morphological with ecological differences. Almost no use has been made of this opportunity up to the present. Oliver (1948) has indeed discussed the ecology and morphology of *Anolis* on Bimini Ids. in the Bahamas but he did not expressly correlate the two. Lundelius (1957) appears to be the only worker who has carefully correlated ecological differences with morphology (in two fence lizards of the genus *Sceloporus*).

In the present paper an attempt is made to correlate morphology and ecology in five species of *Anolis* from Havana, Cuba. The possible effects of introduced *Anolis sagrei* on *Anolis carolinensis* in southern Florida are also assessed.

MATERIALS

Over the past seven years nine trips of one to two weeks' duration have been made to Havana, Cuba, to study the herpetofauna. Two of the trips were in early September and the remainder were in the period from December 19 to January 4.

Field observations have been made on more than twenty specimens of each of the following species: *Anolis angusticeps* Hallowell, *alutaceus* (Cope), *porcatus* (Gray), and *sagrei* (Dumeril and Bibron). The primary reason for using observations from a limited area was to eliminate effects of geographical variation. In addition, one specimen each of *A. argillaceous* Cope and *A. equestris* Merrem, as well as three specimens of an apparently new species of anole were taken. All observations on Cuban species (except *equestris*) are based upon specimens personally collected.

Additional specimens of *A. equestris* from other parts of the province of Havana were used to supplement the single specimen from the study area.

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THE STUDY AREA

The study area extends for about 1700 meters along the west shore of the Rio Almendares in the city of Marianao across the river from Havana. It is a low-lying strip no more than 200 meters wide. An abandoned road, the Carretera del Rio Almendares, runs most of the length of the area and crosses the river just below the Jardines de la Tropical. There is a fairly large field in the northern part of the area and some other smaller clearings in the woodland but most of the area is densely wooded. A cliff about 150 feet high separates most of the area from Marianao. There are some old ruins toward the southern end of the area completely shaded over by large trees. Figure 1 shows a stylized transect of the study area.

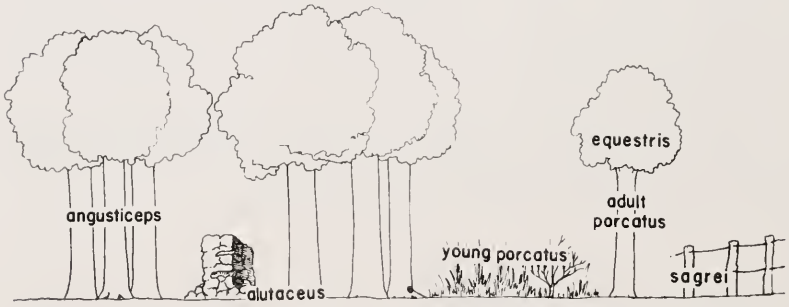

Fig. 1. Stylized cross-section through the study area showing the niche of five species of *Anolis* from Havana, Cuba.

THE SPECIES OF *ANOLIS* STUDIED

The ecology of each species of *Anolis* is described in this section from personal field observations in the study area with supplemental notes from the literature. Data are included on: where each species has been collected; background color; body color; method of locomotion; population density; and interspecies contacts.

Much of this information is summarized in Table I where the species are listed in order of increasing "arboreality." As here used, the more time an animal spends in a tree or the higher up in a tree it is, the more arboreal the animal is considered to be. This is an arbitrary method of distinguishing between habitats without recourse to the creation of a new complex terminology.

Anolis alutaceus (Cope). This small, slender, long-tailed anole is brown with a mid-dorsal tan stripe and a white dewlap. It is limited to a terrestrial niche in woodlands where it is found in three types of habitat: in holes and at the base of the walls of ruins; in rockpiles; and less often among the sticks and leaves of the forest floor. Almost half the specimens were taken on the ground and most of the others were in holes in the walls of the ruins. Three were seen or taken in trees. When approached while in holes, they may turn and retreat up to three feet into the hole or they may hop from the hole down to the ground. Once they land on the ground, they usually hop into the leaves and remain there, often with the head and most of the body hidden beneath the leaves. Part of the tail is usually visible if a careful search is made. One specimen was seen on the low branches of a tree and when chased it did not rely on its protective form and coloration as others have. It used its long hind legs to hop from branch to branch but did not make any attempt to run up, down, or along the branches. None have ever been seen attempting to climb up or down a wall.

An estimate of the relative abundance of *alutaceus* in the area of the ruins was obtained on good collecting days. From 9:40 to 11:55 A.M. on December 29, 1955, seventeen specimens were seen or captured. From 9:40 to 11:10 A.M. on December 23, 1958, six *alutaceus* were collected. There were scattered individuals on the ground elsewhere but they were more difficult to see and catch. No fighting was seen between individuals of this species but this may be due to the fact that they are not usually close together. In the ruins, they may be only a few feet apart, but they are in separate holes and cannot see each other. This species is limited to woodlands that are moderately damp and have a low light intensity. The few body temperatures available indicate that it is active at lower temperatures than the other species studied. Barbour and Ramsden (1919: 154) also report that *alutaceus* is confined to woodlands but note one unusual case of a specimen crossing a hot, dusty road. Within the study area, *alutaceus* comes into contact with *angusticeps* on the walls of the old ruins and with *porcatus,* to a much lesser extent, near the base of some cliffs.

Anolis angusticeps Hallowell. A short-tailed, short-limbed, long-headed anole which is gray or gray-brown with a pale peach-colored dewlap. In the study area, it is limited to a woodland habitat and 17 of 23 specimens were collected on tree trunks two to six feet from the ground. Three specimens were taken on

the walls of the ruins and one was found on the ground. All were taken in moderately moist areas of low light intensity. Individuals rest on tree trunks with the head pointed upwards and when approached remain motionless for a short period but climb quickly if the first attempt to collect fails. Although temperatures were taken in the field on only four specimens, these show the preference of this species for cooler areas. Oliver (1948: 7) observed *A. angusticeps chickcharneyi* only on the upper branches of light gray-colored trees on Bimini, Bahamas. In the study area in Cuba, the species is found on gray or gray-brown tree trunks. Here the abundance of *angusticeps* varies from year to year. In 1957, five specimens were collected in 70 minutes on the morning of December 24 and five more in 30 minutes on the morning of December 27. In 1958, only two specimens were taken in two weeks of collecting. In the study area, *angusticeps* comes into contact with *alutaceus* on the walls of the ruins and with *porcatus* on tree trunks near the edge of the woodlands.

Anolis argillaceus Cope. Only one specimen of this small stocky lizard was taken in the study area. It was collected on December 24, 1957 at 10:35 A.M. among some vines in the crotch of a tree on the border of a clearing. When the vines covering the lizard were moved, the lizard tried to run back under cover rather than up the tree trunk as *porcatus* would, or down to the ground as *sagrei* would have done.

Barbour and Ramsden (1919: 149) report this species as confined entirely to eastern Oriente. This record constitutes a range extension to the west of almost 500 miles.

Anolis equestris Merrem. A large handsome lizard with the upper surface of the head developed into a magnificent bony casque. It is usually a brilliant green and both sexes possess a pink dewlap. The only specimen taken in the study area, a juvenile, was located at a height of six feet in a small tree in a field. Its habitat as noted by Barbour and Ramsden (1919: 133-135) and verified by Kane (personal communication) consists of orchards, palm groves, and trees along roads. None have been seen on the ground, and the majority of specimens have been seen at heights of more than 15 feet in trees. Both sources note fighting on the smooth trunks of the Royal Palm. Light and temperature intensity is greater in these habitats than in the woodland habitat of *alutaceus* and *angusticeps* and somewhat less than in the habitats of *sagrei* and *porcatus*. Kane (personal communication) collected one *equestris* that had partly eaten another anole but the specimen is not available for identification. In laboratory cages, I have

observed mating and other behavior taking place most often on branches rather than on the cage bottom. In the study area, *equestris* can come into contact with *porcatus* and possibly *angusticeps*.

Anolis porcatus (Gray). A long-headed medium-sized anole which has a purplish-pink dewlap. It is found everywhere in the study area except in open fields and deep woodlands. Young are common on small bushes and in tall grass in areas of high light intensity. Adults are found on fence posts and tree trunks. The young are usually green and the adults are usually brown. Currently, it is the commonest lizard in the study area. However, since it is a species preferring edge areas, its great abundance is due in part to man who by breaking up woodland areas and planting trees in open areas, has created an ideal habitat for *porcatus*.

In the study area, *porcatus* seems to be most active in morning and afternoon with a period of decreased activity at midday. This has been noted by Oliver (1955: 133) for the related *carolinensis* during the month of April in Florida where it is most active from 8-11 A.M. and again from 4-6 or 7 P.M. *A. porcatus* probably spends the night in crevices or exposed on bushes or trees. Oliver (1955: 134) has noted this behavior for *carolinensis*. Collections made early in the morning revealed a high percentage of individuals under bark and in crevices in trees. Due to political conditions in Cuba, no collecting could be done at night but one specimen was observed asleep in the fold of a garden plant at night.

Although it is difficult to estimate the abundance of *porcatus* in the study area, the species seems to be found everywhere in favorable habitats. Some indication of its abundance may be gathered from the following field observations. On the trunk of a large fig tree six specimens were collected, and the population on the trunk from the ground to 15 feet up was estimated to be at least 20 lizards. After the first few are collected from one tree, the rest are disturbed, and it is almost impossible to catch all of them. They frequently congregate in large numbers in limited areas, a phenomenon not noted for the other anoles of the study area. For example, under a sign with an area of six square feet, at a height of seven feet above the ground, six to eight specimens were noted at 1:30 P.M. Numbers of *porcatus* may be collected in curled up fronds of broken palm branches that have lodged in another tree. At least 20-30 juvenile to adult *porcatus* along

with one *Hyla septentrionalis* and one *Sphaerodactylus cinereus* were taken from one such palm frond. There were 15-20 in another curled up palm frond. When the palm frond was unfolded, the lizards immediately scurried off in every direction.

While territoriality has been noted for *carolinensis* in Bimini (Oliver, 1955: 111), in the study area, however, large populations found on single tree trunks in December seem to indicate that if territoriality occurs, it is not expressed to any considerable extent at this time of year.

During this study, only one anole was observed feeding. A small juvenile *porcatus* was seen sitting on a weed stalk about four feet from the ground in a clearing. It crept slowly toward the end of the stalk and grabbed a resting dragonfly.

In the study area, *porcatus* comes into contact with *sagrei* frequently on fence posts. It also meets *angusticeps* in areas bordering dense woodland and probably also contacts *equestris* farther up in trees.

Since specimens of *A. carolinensis* Voigt in the Cornell University Herpetology Collection from the Fort Myers-Bonito Springs area of southwestern Florida and from Key West were examined in order to study the effects of populations of *sagrei* upon *carolinensis*, a few remarks on this species are inserted here to provide a proper comparison with *A. porcatus*.

Anolis carolinensis Voigt. This species is native to the United States, is a smaller representative of the Cuban *porcatus*, and is probably correctly considered as conspecific with *porcatus* (Oliver, 1948: 12). I have observed this species only casually in North Carolina and in Miami, Florida. From these observations and from the literature, it is apparent that *carolinensis* occupies both terrestrial and arboreal habitats though perhaps preferring the latter. Duellman and Schwartz (1958: 279) give the optimum habitat in southern Florida as mesophytic hammocks, or in cultivated areas in gardens and shrubbery around houses. The dewlap is rose-pink to red and the body color varies within a wide range of browns and greens. Over most of its range, *carolinensis* does not come into contact with any other member of the genus. However, on Key West and around several cities in southern Florida, it does come into contact with introduced populations of *A. sagrei*.

Anolis sagrei (Dumeril and Bibron). This long-legged, short-headed, alert anole has an orange-red dewlap and can change color within a wide range of browns from pale tan to almost

black. It is the common lizard of the roadside and open field. The juveniles and females are found mostly on the ground or a short distance from the ground among weeds. Adult males are usually found singly on observation perches at the top of woodpiles or on fence posts. Schwartz and Ogren (1956: 98), Barbour and Ramsden (1919: 143), Barbour (1904: 58, and 1914: 286), and Oliver (1948: 25) all report on its great abundance on the ground, brush, fallen logs, and boards, fence posts, and piles of debris. In the study area *sagrei* is second only to *porcatus* in abundance. Evans (1938) notes that *sagrei* males defend territories from other males of the same species; no attempt was made to verify this in the study area. However, two males were never taken on the same fence post and only rarely on the same telephone pole. When an attempt is made to approach *sagrei* on fence posts, they quickly retreat to the ground and swiftly run away. This has also been noted in the Cayman Islands by Grant (1940: 29) and on Bimini, Bahamas, by Oliver (1948: 25). The males always face downwards while on fence posts which indicates that their food is terrestrial. Evans (1938: 103) notes that they make frequent forays for insects in all directions from the observation perches on fence posts. My field observations show that *sagrei* becomes active somewhat later in the day than *porcatus* and has a peak of activity in the middle of the day. Collections from 8 to 10 A.M. have revealed that some individuals are partially active under rocks. They probably spend the night under rocks and other such cover. In the study area, *sagrei* comes into contact only with *porcatus* at the base of trees and fence posts.

Anolis sp. Three specimens of a medium-sized white-throated anole were also taken from the study area. They seem to resemble *A. carolinensis* most closely. Nothing is known of their ecology since they were not individually tagged in the field. They will be treated in a subsequent paper.

Associated Herpetofauna. Since they are part of the total ecology of the study area, the following list of herpetofauna is presented. Amphibians: *Rana catesbeiana* (one adult and many tadpoles of this introduced species taken in backwaters of the Rio Almendares); *Hyla septentrionalis* (common in holes in trees); *Eleutherodactylus atkinsi atkinsi, E. cuneatus, E. ricordii planirostris*[1] (abundant under rocks throughout the study area). Turtles: *Pseudemys decussata* (common on rocks in the Rio Almendares). Lizards: *Hemidactylus mabouia* (at night near

[1]These *Eleutherodactylus* were determined by Mr. Benjamin Shreve.

house lights); *Gonatodes fuscus* (on logs and trees); *Sphaerodactylus notatus* (under debris throughout the study area); *Sphaerodactylus cinereus* (under bark of trees throughout the study area); *Leiocephalus cubensis* (common in edificarian situations near the study area); *Amphisbaena cubana* (a few individuals under debris in open areas). Snakes: *Arhyton vittatum* (a few specimens under rocks); *Tretanorhinus variabilis* (a juvenile under a car tire on the river shore); *Alsophis angulifer* and *Dromicus andreae* (a few in a field several years ago before it became overgrown); *Typhlops lumbricalis* (fairly common under rocks); *Tropidophis maculatus* (few) and *Tropidophis pardalis* (common) (both species under rocks and other debris).

Most of these species probably have little effect on the *Anolis* in the study area. *Tropidophis* is the most important member of the associated herpetofauna since both *T. maculatus* and *T. pardalis* include *Anolis* in their diets. Both *A. alutaceus* and *A. angusticeps* have been found in the stomach of a *T. maculatus*. In the laboratory, both species of *Tropidophis* feed on *A. porcatus* and *A. sagrei* without hesitation. Captive *Alsophis* also feed on *Anolis* but these snakes are not present in large enough numbers to have much effect on the *Anolis* population.

SPECIES INTERACTION

Indications of fluctuations in populations of *porcatus* were noted within the study area over a period of a few years. The Carretera del Rio Almendares is lined, for part of its length, with fence posts. In the years when all the grass around the posts was cut down, *sagrei* was the most common lizard on the fence posts. In years when there was tall grass in the field behind the posts, and no grass along the road in front of the fence posts, some *sagrei* and some *porcatus* were present on the posts. In the last few years, some of the fence posts have taken root and furnish shade in the areas. With this change, *sagrei* has decreased and *porcatus* has increased in numbers on these living fence posts. In nearby areas, tall grass sometimes completely surrounds fence posts, and neither *sagrei* nor *porcatus* are present.

Although *sagrei* and *porcatus* are found on fence posts, they usually occupy different positions. Typically adult male *sagrei* are located facing downward on the lower part of the fence post no more than a few feet from the ground. On the same fence post, *porcatus* is found facing upwards on the upper part of the fence post. If one species is absent, the other will tend to occupy the entire fence post, but in all cases, *sagrei* faces downward and

porcatus upward. In the Cayman Islands this has also been noted (Grant, 1940: 28) between *A. sagrei ordinatus* and *A. maynardi* (considered conspecific with *porcatus* by Barbour, 1937: 119). It is difficult to force *porcatus* to go down or *sagrei* to go up a fence post. When a line of fence posts was approached, each *sagrei* ran down the fence post into the leaves. A juvenile *porcatus* was observed to run to the top of a fence post and then to jump to two more fence posts in succession rather than move down the fence post. If placed on the ground, *porcatus* seems uncomfortable and it quickly moves to a nearby tree or fence post and climbs to safety. When approached by an observer, an adult *porcatus* which is on a tree will warily circle upwards around the tree putting the trunk between itself and the collector. This has also been noted by Oliver (1948: 16) for the related *A. carolinensis lerneri* on Bimini.

The Florida situation requires special attention. Populations of *sagrei* now exist on Key West and adjacent keys and in several mainland areas. The populations on the keys (*A. sagrei stejnegeri*) have apparently reached there by natural means. The mainland populations are recent introductions by man. Oliver (1950: 56) reports that Cuban *A. s. sagrei* have been introduced into the Tampa area. *A. sagrei ordinatus* have been introduced from the Bahamas into the Lake Worth area (Oliver, 1950: 56) and reported from Miami (Bell, 1953: 63). Duellman and Schwartz (1958: 283) refer the Miami populations to *A. sagrei stejnegeri*. Willis (1953: 74) reports *A. s. sagrei* from Coral Gables and Miami. At any rate, there are populations of the aggressive, terrestrial *sagrei* in contact with *carolinensis* in a number of areas in southern Florida. From studies by Oliver (1950), Neill (1951), Bell (1953), and Duellman and Schwartz (1958), it is apparent that the ecology of *sagrei* in regions of sympatry with *carolinensis* does not differ noticeably from *sagrei* in the study area in Cuba.

LAMELLAE

One of the most obvious differences in ecology of the *Anolis* species studied is relative arboreality (Table I). (See the definition above.)

The digital expansions of *Anolis* like those of geckos are undoubtedly adaptations to the generally arboreal habits of the genus. Differences in the extent of arboreal habit might consequently be expected to imply differing degrees of perfection and

efficiency of these arboreal adaptations. Certainly the width of the digital expansion appears to correlate roughly with the degree of arboreality. However, this is a character difficult to make objective (See Fig. 2).

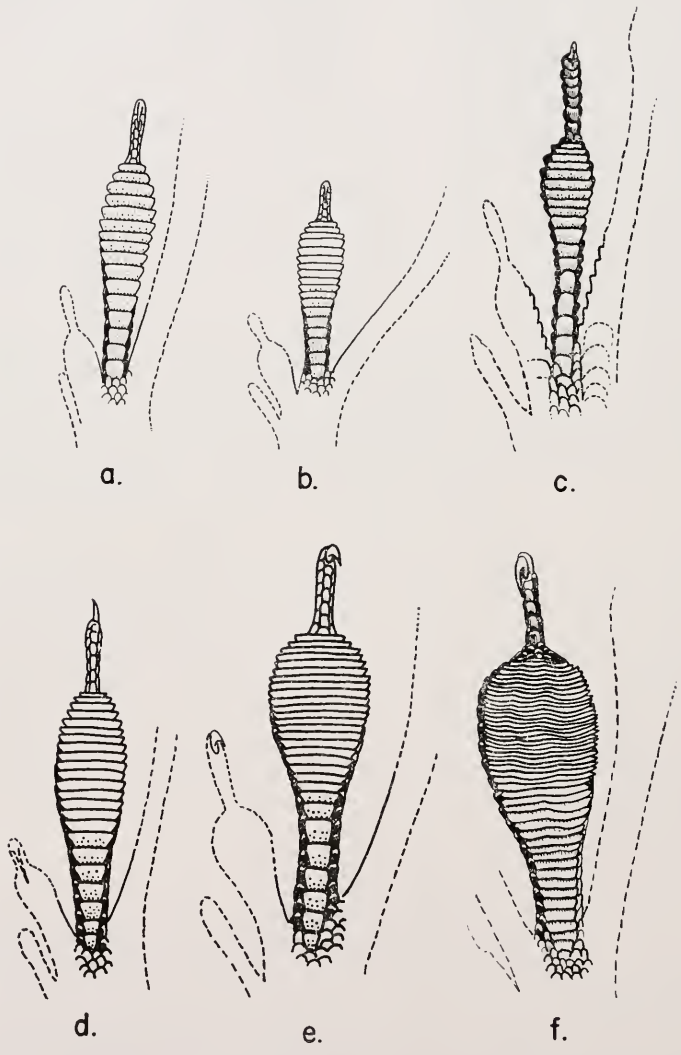

Fig. 2. Feet of six species of *Anolis* showing the lamellae on the third toe of the left hind foot. (a) *alutaceus*, (b) *angusticeps*, (c) *sagrei*, (d) *carolinensis*, (e) *porcatus*, (f) *equestris*. Not to scale.

Another conspicuous character of the digital expansion may, however, be quantitatively recorded — the number of lamellae. The correlations of this character have therefore been examined.

Counts were made of the lamellae of the third and fourth toes of the right front foot and the third toe of the right hind foot, of the *Anolis* from the study area, plus samples of *A. carolinensis* from Florida. These toes were selected because they have large numbers of lamellae and therefore seem to be important in bearing the weight of the lizard and are likely to show variation between species, and because counts can be made accurately since there is usually a distinct break between the lamellae of the toes and the scales of the foot. Counts were not made on the fourth hind toe because the distinction between lamellae and foot scales is less evident there. Enlarged lamellae-like scales on the foot were not counted. In the few cases where the proximal lamellae on the toes were divided, the divided lamellae were counted as one. Frequency distributions of the lamellae on each of the toes are presented in Tables II and III.

From the data thus obtained, three factors appear to be correlated with lamellae number. There is a positive correlation between lamellae number and body size (Table IV). This relationship is understandable because as the length of the lizard increases, the volume and presumably the weight increases as the cube while the area of the toes increases as the square. The increased number of lamellae in larger species compensates for the loss in toe area relative to weight. Hecht (1952: 118) has also shown a positive correlation between lamellae number and body size in species of *Aristelliger*. A second factor is that of sexual dimorphism. In the study area, except for *A. equestris* and *A. alutaceus*, male anoles have significantly more lamellae than females (Table IV). But this too may be a function of size since (except for the two species mentioned above) male anoles are larger than females (Table IV).[1] However, this rule does not appear to apply to Key West *carolinensis* in which, despite the larger size of males, there is no significant difference in lamellae number between males and females. Unless there is an ecological difference between males and females, this is difficult to explain. Thirdly, there appears to be a correlation between number of lamellae and arboreality as it has been defined above. The more arboreal species have more lamellae (Table IV). However, here

[1]But see ♀ *angusticeps* compared with ♀ *sagrei* below.

also there is some ambiguity. In general the more arboreal anoles are also larger.[1]

Increased numbers of lamellae could be ascribed wholely to the larger body size of arboreal species. However, there are several lines of evidence that suggest that there may be a real rather than a spurious correlation between arboreality and number of lamellae.

In *A. porcatus,* the young are found in a bush-grass habitat while adults are limited to a fence post-tree habitat. Superficial examination indicates that the toes become wider with age but more data is needed. There is no evidence of changes after hatching in lamellae number. The possibility of the phenomenon of

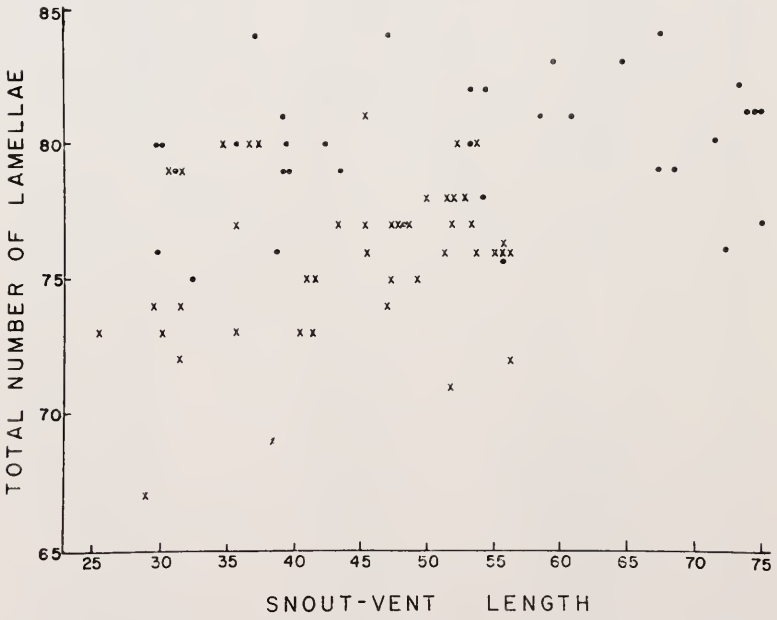

Fig. 3. Total number of lamellae on the third and fourth toes of the right front foot and the third toe of the right hind foot of *Anolis porcatus* from Havana, Cuba. The dots represent males and the crosses females.

[1]Within a lizard genus, the more arboreal member of a group of sympatric species tends to be the larger. Within the study area, *porcatus* is larger than *sagrei*; *angusticeps* is larger than *alutaceus*: and *equestris,* the most arboreal of all, is the largest one. Studies in progress on the gecko *Sphaerodactylus* also show the arboreal *cinereus* to be larger than the terrestrial *notatus*. Smith (1946: 204, 222) has shown that the arboreal *Sceloporus olivaceus* is larger than the terrestrial *S. undulatus*. The significance of this trend is difficult to see.

wider variability in juveniles than in adults was tested in two ways. The total number of lamellae on the three toes counted was plotted against snout-vent length (Fig. 3). Until sex was taken into consideration, it appeared that the mean number of lamellae did increase with size classes, as found by Hecht (1952: 117) in *Aristelliger*. But this was due primarily to sampling bias. There are more males in the largest size groups and more females in the smallest size groups so the differences in mean numbers of lamellae are mostly an expression of the number of each sex in a given size group.

Specimens of *A. porcatus* for which both exact ecological data and lamellae counts are available fall into two ecological niches: (1) bushes and grass; (2) fence posts plus trees. For both sexes there is an increase in body size from the first to the second group (Table V). The mean number of lamellae in the bush-grass habitat is significantly lower than that for the fence post plus tree habitat. Thus, with a shift in habitat, there is a change in the distributions of body size and lamellae number which seems to be due to selection acting against individuals with low lamellae numbers. Selection acts not when a certain size is reached, but when the young make the habitat shift to fence posts and trees.

If lamellae number is plotted against snout-vent length for *sagrei*, a similar picture is obtained (Fig. 4). The main difference between the lamellae-body size relations in the two species is the greater separation between males and females in *sagrei*. However, only the male *sagrei* make a habitat shift, while in *porcatus* both sexes shift. Therefore, part of the male-female difference in *sagrei* may be due to the larger maximum size that the male reaches but part of it may be correlated with the fact that adult male *sagrei* are found on fence posts while the females and juveniles of both sexes are limited to life on the ground.

Comparison of female *angusticeps* with female *sagrei* also supports the correlation of arboreality with increased numbers of lamellae. Female *sagrei* are larger (mean 34.5mm, max. 44.4mm) than *angusticeps* (mean 32.5mm, max. 38.9mm) but *angusticeps* females have a larger mean and maximum number of lamellae. Female *sagrei* are almost completely terrestrial WHILE FEMALE *angusticeps*, LIKE THE MALES, ARE ARBOREAL.

A fourth case bears on the question of climbing ability and lamellae number. *A. carolinensis* of Florida is closely related to the Cuban *porcatus* and since it has no anole competitor over

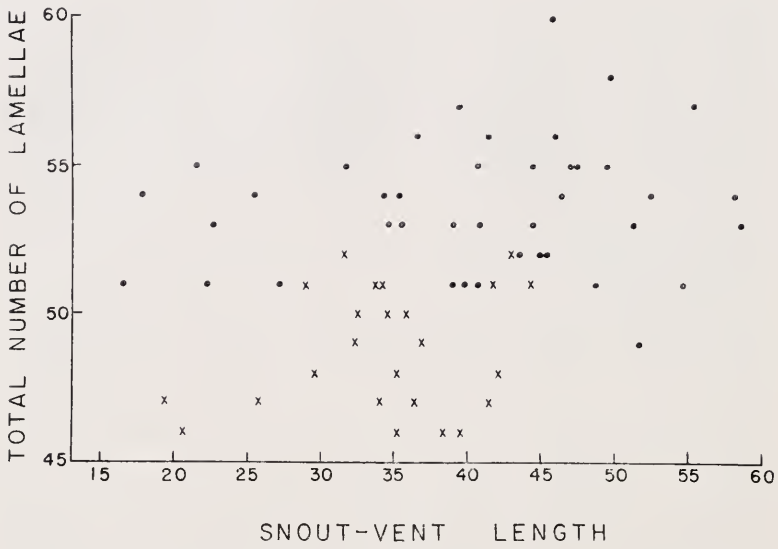

Fig. 4. Total number of lamellae on the third and fourth toes of the right front foot and the third toe of the right hind foot of *Anolis sagrei* from Havana, Cuba. The dots represent males and the crosses females.

most of its range it is able to occupy all suitable anole habitats, both terrestrial and arboreal. Both in lamellae number and body size it is intermediate between two Cuban species — the arboreal *porcatus* and the terrestrial *sagrei* (Table IV). As discussed above, *sagrei* has become established in a number of areas where *carolinensis* is present. Theoretically the aggressive, terrestrial *sagrei* should tend to drive the more generalized *carolinensis* out of the terrestrial part of its habitat. There then should be strong selective forces favoring those *carolinensis* with higher lamellae numbers, since they can better utilize the arboreal part of the habitat. Counts on a small series of *carolinensis* from Key West, an area of long contact with *sagrei*, are indeed higher than counts from an area where they are not in contact (Fort Myers-Bonito Springs), as shown in Table IV. These differences are significant at the 99 per cent level for males and females (t values of 2.85 and 4.67 respectively). This is not conclusive evidence that the suggested theory is correct because there is the possibility that the lamellae numbers are correlated with greater body size, geographic variation in the latter character being the controlling

factor. Evidence for or against the theory can only be obtained from study of *carolinensis* over a period of years in an area where *sagrei* has been recently introduced.

TAIL LENGTH

Tail length was measured to the nearest tenth of a millimeter from the vent to the tip of the tail. All specimens were carefully examined and individuals with broken or regenerated tails were excluded. Tail length was then divided by snout-vent length. *A. alutaceus* has a much longer tail than the other species studied (Fig. 5). This seems to be correlated with its use as a balancing

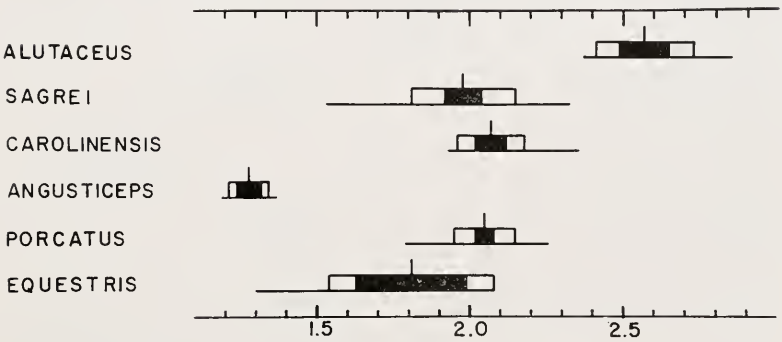

Fig. 5. Ratio of body length to tail length in six species of *Anolis*. The horizontal line represents the range, the vertical line the mean, the filled-in rectangle two standard errors on each side of the mean, and the open rectangle one standard deviation on each side of the mean.

organ as this species hops along the forest floor. *A. angusticeps* has a much shorter tail than the other species, possibly correlated with the slow deliberate movements of this species. The other tree-trunk dweller, *porcatus*, has a longer tail than *angusticeps*, possibly because as a juvenile it makes daring leaps from leaf to leaf and uses its tail as a balancing organ. All the arboreal species have the base of the tail somewhat thickened for use as a prop in climbing. This adaptation is not found in the terrestrial *sagrei* and *alutaceus*. The tail of the former is compressed while that of the latter is rounded and slender, well adapted for holding up in the air as a balancing organ while the lizard hops.

HIND LEG LENGTH

Hind leg length was measured to the nearest tenth of a millimeter from the anterior insertion of the thigh to the tip of the toenail of the longest toes with the leg extended at right angles to the body. Dividing hind leg length into snout-vent length provided the ratio on which comparisons were based. The larger arboreal species have shorter legs (Fig. 6). They move about

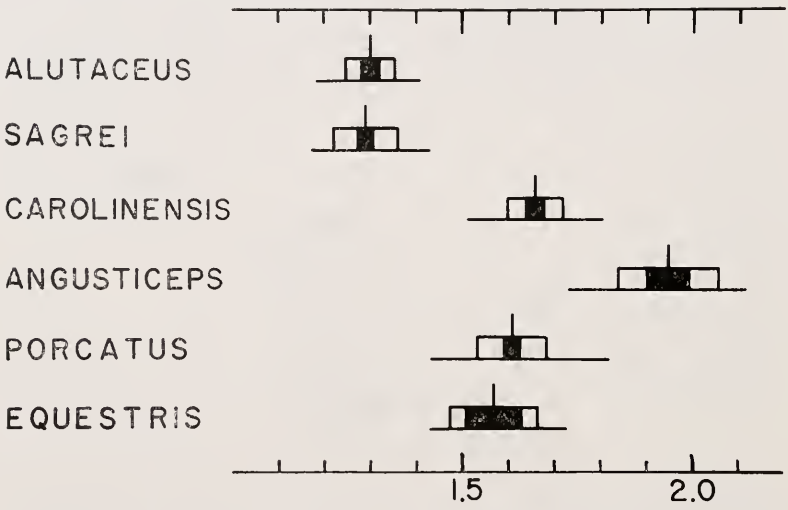

Fig. 6. Ratio of hind leg length to body length in six species of *Anolis*.

more slowly in the trees than the terrestrial species do on the ground. The long-legged terrestrial *sagrei* runs swiftly about in fields while the long-legged *alutaceus* employs its long hind legs in hopping on the forest floor. Lundelius (1957 : 80) reported that the terrestrial *Sceloporus undulatus* has longer legs than the arboreal *S. olivaceus*.

COLOR

Another adaptation to be considered is the ability of *Anolis* to change color. The two terrestrial species, *sagrei* and *alutaceus*, are limited to color and pattern shifts within a range of browns. The ability to turn green would be of no positive advantage against their brown backgrounds and would be selected against.

The arboreal *angusticeps* varies within a range of grays, gray-browns, and gray-greens, the colors which are present on the tree trunks of its damp woodland habitat. *A. porcatus* and *carolinensis* have the ability to change color within a wide range of greens and browns. Young *porcatus* are found among the leaves of shrubs and bushes where they are usually green. Adults are usually found on the trunks of large trees in diffuse daylight where they are usually brown.

The range within which a species can change color thus appears to be adaptive to their ecological niche (Table I). Hadley (1929: 110) notes that *porcatus* is green at night, brown in diffuse daylight, and green in direct sunlight. Color changes are primarily associated with changes in light, temperature, humidity, and emotional state, but in most cases they result in the lizard matching its background in nature (Van Geldern 1921: 81-87). An exception is found where bright green *porcatus* (and *carolinensis* in Florida) stand out against the brown of telephone poles and isolated trees in situations modified by man. But perhaps this is a habitat only recently colonized so there has been little time for selection to act and few predators to provide selection pressure.

As for the completely arboreal *equestris,* both Kane (personal communication) and Barbour and Ramsden (1919: 134) indicate that this species is normally green. Hadley (1929: 112) notes that *equestris* is normally green in diffuse light, the most frequent condition in its niche.

PERITONEAL PIGMENTATION

Differences in the distribution of black pigment in the peritoneal cavity are present in the species of *Anolis* studied. Black pigment is almost completely lacking in *alutaceus.* All the rest have at least a pigmented parietal peritoneum. In *angusticeps,* additional pigment is sometimes present on the ventral mesentery that suspends the liver. Both *porcatus* and *carolinensis* have additional pigment on the mesocolon and mesoduodenum. The latter also has pigment on the ventral mesentery of the liver. The pigment distribution is similar in *equestris* but does not extend into the most anterior portion of the peritoneal cavity. There is still more pigment in *sagrei*; it covers the entire large and small intestines and extends onto the testes of the male.

Oliver (1948: 28) has noted similar conditions in the Bimini *A. angusticeps chickcharneyi, carolinensis lerneri,* and *sagrei ordinatus,* but offers no suggestions as to the possible significance

of these differences. There would appear to be a rough correlation of the amount of peritoneal pigmentation with the amount of radiation to which the lizard is exposed. The species of the deepest woodland, *alutaceus*, lacks pigment and the other woodland species, *angusticeps*, has only a slight amount. The three species of more open areas, *equestris*, *carolinensis*, and *porcatus*, are exposed to greater radiation intensities and have more pigmentation. *A. sagrei* prefers open fields and has the most pigmentation. It is possible that this pigmentation serves as protection against harmful solar radiation as Klauber (1939: 77) has proposed for reptiles in the southwestern United States. Even though Bodenheimer (1954) and Hunsaker and Johnson (1959) have indicated that the skin of some reptiles is impervious to various forms of radiation, no alternative to Klauber's explanation has yet been proposed.

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SUMMARY

This paper has attempted to correlate ecology with morphology in six species of *Anolis* from southern Florida and Havana, Cuba. It is felt that with proper ecological data, valid correlations can be made that can lead to an appreciation of the significance of characters often used in taxonomic analysis. Also, light is shed upon the structural adaptations that allow related sympatric species to occupy the same geographical area without facing deleterious competition. It has been shown that selection has acted so that lizards will usually match the color of their natural

background. Examples have been shown to support the idea that peritoneal pigmentation is connected with exposure to radiation. The value of long legs to terrestrial lizards has been shown. Short relative tail length has been correlated with arboreality. The more arboreal members of a group of sympatric species have been shown to be larger and have more lamellae than terrestrial species. Data have been presented to support the contention that increased numbers of lamellae are an adaptation to increased arboreality.

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TABLE I

Summary of ecological data for six species of *Anolis* from southern Florida and Havana, Cuba. The species are listed down the page in order of increasing arboreality.

Species	Habitat	Background Color	Body Color
alutaceus	On the ground or in holes in walls	Brown	Brown
sagrei	On the ground but adult males frequently on fence posts, etc. near the ground	Brown or gray	Brown-gray
carolinensis	In trees and on the ground	Green; brown	Green; brown
angusticeps	On tree trunks	Gray	Gray-brown
porcatus	Young — in bushes and grass Adults — on tree trunks and fence posts	Green Brown	Usually green Usually brown
equestris	High up in trees	Green	Green

TABLE II

Frequency distributions of the lamellae on the third and fourth toes of the right front foot and the third toe of the right hind foot of females of six species of *Anolis* listed across the page in order of increasing arboreality.

Species	*alutaceus*			*sagrei*			Mainland *carolinensis*			Key West *carolinensis*			*angusticeps*			*porcatus*			*equestris*		
N		15			24			11			9			14			44			7	
Foot	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H
Toe	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3
No. lamellae																					
12			4																		
13	4		6																		
14	10		5			1															
15	1	2		4	5	8							3		2						
16		9		10	4	10							8		7						
17		2		7	13	3	1	1	2	1		2	2		3						
18		2		3	2	2	4	1	4	1		—	1	7	2						
19							5	6	3	1	2	4		6							
20								3	2	5	3	3		1							
21										1	3					1					
22											1					1	1				
23																5	—	1			
24																14	6	7			
25																14	13	10			
26																7	11	16			
27																1	10	8			
28																	2	2			
29																	1				

TABLE II (cont.)

| | | |

TABLE III

Frequency distributions of the lamellae on the third and fourth toes of the right front foot and the third toe of the right hind foot of males of six species of *Anolis* listed across the page in order of increasing arboreality.

							Mainland			Key West											
Species	*alutaceus*			*sagrei*			*carolinensis*			*carolinensis*			*angusticeps*			*porcatus*			*equestris*		
N		9			41			22			14			8			34			3	
Foot	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H
Toe	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3
No. lamellae																					
13	3		1																		
14	6		8																		
15																					
16		3		3	1	5							1		1						
17		4		8	9	15	1						6		7						
18		2		20	13	15	3		5	2	1	4	1								
19				8	16	4	12	6	11	2	5	2		3							
20				2	2	1	4	8	2	7	2	5		4							
21							2	7	3	2	3	2		1							
22								1	1	1	2	1									
23											1					1					
24																6					
25																5		4			
26																15	4	9			
27																5	16	11			
28																2	11	6			
29																	3	4			
35																			1		
36																			—		
37																			1	1	
38																			—	—	
39																			—	—	
40																			—	1	
41																			1	—	2
42																				1	—
43																					—
44																					—
45																					—
46																					1

TABLE IV

Correlation between body size and lamellae number in six species of *Anolis* from southern Florida and Havana, Cuba. The species are arranged down the page in order of increasing arboreality.

Species			Body Length	Lamellae Number				"t" value
	Sex	N		$\overline{X}$		$\overline{X}$	Variance	between sexes
alutaceus	♀♀	15	16.1- 39.4	29.23	40- 46	43.13	2.41	N.S.
	♂♂	9	16.0- 36.6	30.92	42- 46	44.44	1.53	
sagrei	♀♀	24	19.4- 44.4	34.47	46- 51	48.75	4.28	10.67**
	♂♂	41	16.5- 58.6	40.69	49- 60	53.66	5.03	
carolinensis (Mainland of Florida)	♀♀	11	27.4- 44.3	38.61	51- 58	55.91	3.20	3.19**
	♂♂	22	40.5- 56.5	49.42	55- 64	58.55	5.69	
carolinensis (Key West)	♀♀	9	44.3- 50.5	46.32	56- 64	60.67	6.50	N.S.
	♂♂	14	42.7- 59.1	54.16	55- 66	61.14	9.36	
angusticeps	♀♀	14	17.1- 38.9	32.51	49- 54	51.00	2.31	4.36**
	♂♂	8	34.1- 42.1	38.66	53- 56	53.63	0.99	
porcatus	♀♀	44	25.4- 56.4	44.24	67- 81	75.84	9.16	6.49**
	♂♂	34	29.7- 75.1	52.45	75- 84	79.97	5.61	
equestris	♀♀	7	83 -161	117.3	112-126	120.14	22.81	N.S.
	♂♂	3	149 -154	151.3	113-125	120.00	39.00	

** significant at the 99% level

TABLE V

Change in distributions of total number of lamellae and body size with habitat shift in *Anolis porcatus* from Havana, Cuba.

	Bush-Grass Niche					Tree-Fence Post Niche					
	Snout-vent length			Lamellae No.		Snout-vent length			Lamellae No.		
	N	Range	$\bar{X}$	Range	$\bar{X}$	N	Range	$\bar{X}$	Range	$\bar{X}$	"t" value
♀♀	6	29.0-56.4	38.4	67-77	73.0	18	31.4-56.0	45.4	71-81	76.2	3.24**
♂♂	6	29.7-48.4	36.6	75-81	77.3	15	35.7-75.1	55.8	77-84	80.7	2.22*

* significant at the 95% level
** significant at the 99% level

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
VOL. 125, NO. 6

CRANIAL ANATOMY OF THE CYNODONT REPTILE *THRINAXODON LIORHINUS*

BY RICHARD ESTES

WITH TWO PLATES

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
AUGUST, 1961

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No. 6 — Cranial anatomy of the cynodont reptile Thrinaxodon liorhinus

By Richard Estes[1]

The material discussed here was collected by the 1947 University of California African Expedition, Southern Section, at Harrismith, Orange Free State. The locality data is as follows: from Harrismith, six miles on the Bezuitenhout Pass road, then two miles east to a farm, and one mile north to old stone corrals on the point of a hill overlooking the river. These skulls were picked up as nodules, which occur on the west and north slopes of this point. The collectors were Dr. and Mrs. Charles L. Camp. The locality is in the early Triassic *Lystrosaurus* zone, and is designated University of California Vertebrate Locality number V-36115.

The specimens dealt with below include two juvenile skulls, which bear University of California nos. 42877 and 42878, and two adult skulls, U. C. nos. 40466 and 42865. The juvenile skulls were prepared by the use of ten per cent acetic acid and treatment with Glyptal as described by Brink (1957b). They are both crushed dorsoventrally, and lack the postorbital bars. Badly crushed and broken lower jaws are also associated with each of these skulls. U. C. no. 40466 is a fully adult skull: its preservation is perfect and undistorted, and very little is missing. It was manually prepared by Mr. Martin Caulkin, whose careful work on this specimen is gratefully acknowledged. The other adult specimen is somewhat smaller, and is also well preserved and nearly complete, but is slightly distorted. It was also prepared in acid as described above to expose the basicranium and the inside of the cranial cavity.

THE JUVENILE SKULLS

Brink (1955) has described an association of an adult and a juvenile skull of *Thrinaxodon liorhinus* found together in the same nodule. The juvenile skull is incomplete behind the orbits. Juveniles are uncommon in the fossil record and the completeness of the University of California specimens warrants a description supplementary to that of Brink.

The description is based on both skulls, and unless otherwise stated, the characters are preserved on both specimens.

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Snout

The premaxillae are missing in no. 42878 and are incomplete in no. 42877, but in the latter the usual four incisors are present on each side. The septomaxilla is well developed, and has a posterior process inserted into the maxillo-nasal suture, a dorsal intrafenestral process, and a ventral palatine process. The prominent septomaxillary foramen is relatively larger than that of the adult.

The nasals resemble those of larger individuals in being narrow anteriorly and pitted with tiny foramina. Posteriorly they expand and articulate with the frontals, prefrontals, and lacrimals, though this region of the nasals is not as much expanded as in the adults.

The maxilla has the usual shape and contacts, and is also strongly pitted with foramina. The teeth will be discussed below.

Skull Roof and Temporal Region

The frontals and parietals are relatively broader than those of the adults, and the parietals lack a sagittal crest. The temporal crests remain discrete throughout their length; between them the flattened cranial roof is narrowest just posterior to the nearly circular parietal foramen. The frontal differs in both specimens from the condition characteristic of adult *Thrinaxodon liorhinus* as follows. Each frontal sends a median process into the midline suture between the nasals, forming a wedge or arrow-shaped fronto-nasal suture instead of the usual transverse one. The prefrontal-frontal and fronto-nasal sutures thus form almost a straight line. Brink (*in litt.*, 1958) has informed me that his specimen also shows this condition, but to a much lesser degree; thus the sutures mentioned above meet at a greater angle.

The prefrontals are small and just touch the postorbitals. The latter are fragmentary, but indicate that the posterior extent of the postorbital was at the fronto-parietal suture or a little posterior to it. The postorbital bars are broken away. The jugals and squamosals closely resemble those of the adults.

The right quadrate is present on no. 42877, but it is badly crushed, and only a tiny dorsal spike of the quadratojugal remains in its groove in the squamosal.

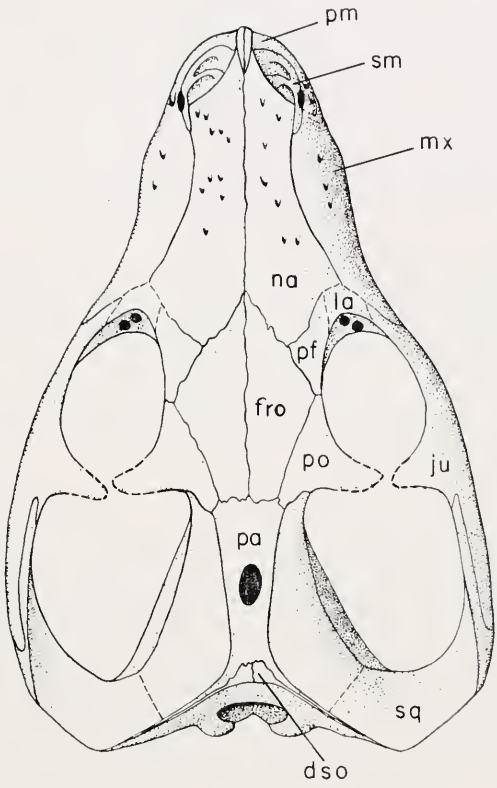

Fig. 1. Dorsal view of restored juvenile skull of *Thrinaxodon liorhinus*; X about 2.5. Abbreviations: *aam*, anterior ampulla; *avsc*, anterior vertical semicircular canal; *bo*, basioccipital; *bs*, basisphenoid; *cc*, crus communis; *coch*, cochlea; *cr*, cochlear recess; *dso*, dermosupraoccipital; *ec*, ectopterygoid; *eo*, exoccipital; *ep*, epipterygoid; *fj*, jugular foramen; *fo*, fenestra ovalis; *fr*, fenestra rotunda; *fro*, frontal; *ic*, internal carotid foramen; *ir*, interpterygoid vacuity; *ju*, jugal; *la*, lacrimal; *m*, muscle scar; *ml*, median line; *mx*, maxilla; *na*, nasal; *op*, opisthotic; *pa*, parietal; *pam*, posterior ampulla; *pf*, prefrontal; *pl*, palatine; *pm*, premaxilla; *po*, postorbital; *pr*, prootic; *ps*, parasphenoid; *pt*, pterygoid; *pvsc*, posterior vertical semicircular canal; *qj*, quadratojugal; *qu*, quadrate; *sm*, septomaxilla; *sq*, squamosal; *sr*, saccular recess; *st*, stapes; *t*, parasphenoid teeth; *vf*, venous foramen; *vo*, vomer.

Occiput

The occiputs of both juvenile specimens are crushed, but the tabulars and dermosupraoccipitals are visible. In 42878 the right half of the dermosupraoccipital is missing along what is probably a suture, and 42877 shows a distinct suture in this region, indicating that the bone was paired. The posttemporal foramen is relatively a little larger than in the adult.

Lower Jaws

The lower jaws are badly crushed and broken in both specimens; no tooth counts could be made and no attempt has been made to figure or restore either jaws or teeth.

The angulars are relatively a little larger and more flattened externally than in the adults. The angular flanges are broken away in both specimens.

Teeth

The juvenile thrinaxodons have a greater number of teeth than do the adults, though the form of the tooth is very similar. Brink's juvenile specimen (Brink, 1955) shows seven teeth on the right side. No. 42877 has seven teeth on both sides, and possibly eight on the left side. No replacement is noticeable in the incisors, though all are quite loose in their sockets. The canines are relatively small. The first three postcanine teeth on the left side of no. 42878 are unicuspid and falciform, unlike the tricuspid adult teeth of comparable position. On the right side of no. 42878 the fourth tooth is being replaced; the tip of the replacing tooth is barely emerging from the socket, although on the left side it seems to be completely erupted. The replacing tooth on the right is bicuspid, unlike the comparable tooth in the adult, which is tricuspid. The sixth tooth on the right side is large and has slipped down out of its socket. On the left side six postcanine teeth are present, none of which seem to show any sign of replacement. However, the canine protrudes only slightly from the alveolus and is apparently just erupting.

Teeth in adult specimens are much larger than those of the juveniles. Replacement teeth in the juvenile are very little larger than those replaced, indicating that further replacements would be needed to bring the teeth up to the adult size. Brink (1955, pp. 75-76) came to the same conclusion on the basis of his small

skull, and Crompton (1955, p. 665) has shown that some higher cynodonts also have multiple (i.e. non-mammalian) tooth replacement.

Palate and Basicranium

The palate and basicranium are fairly well preserved on both specimens, but are more complete in no. 42877. The secondary palate is as well developed as in fully adult *Thrinaxodon liorhinus;* the maxillae and palatines meet on a long midline suture. A posterior palatine foramen is present on the maxillopalatine suture. The ectopterygoid is not preserved, but a matrix-filled cavity on no. 42878 indicates that this bone was very small. There is a large palatal roof component of the vomer, dorsal to the choanae, but the median process which would have reached to the secondary palate is broken away.

In contrast to adult cynodonts, the pterygoids enclose a small interpterygoid vacuity on each side of the cultriform process of the parasphenoid. Dorsally the basipterygoid processes are smooth, and articulate on correspondingly smooth vertical faces of the pterygoids, just forward of the internal carotid foramina; ventrally, the median ridges of the pterygoids curve mediad, do not meet the cultriform process, and have a digitate suture with the basipterygoid processes. The ventral keels of the anterior portions of the pterygoids are not continued posteriorly onto the rounded basipterygoid tubera. The pterygoids continue posteriorly, but are broken before reaching the quadrates.

The basisphenoid and parasphenoid are fused, except at the anterior end of the basisphenoid dorsally, where a slight separation is present in the region of the trabecular attachment to the basisphenoid, as described by Parrington (1935b, p. 400). The tip of the cultriform process of the parasphenoid is sutured anteriorly to the pterygoids, and the process extends posteriorly between the interpterygoid vacuities. At this point the cultriform process bears a ventral keel, and in the region between the prominent internal carotid foramina, it expands and bears five small teeth on a roughened area. From this area, the wings of the parasphenoid expand and pass back over the basioccipital in a squamous suture, the full extent of which is obscured by breakage. There is a small gap between the basioccipital and basisphenoid, which was undoubtedly filled with cartilage.

The basioccipital is a hexagonal bone, and bears paired oval depressions on the ventral surface, which were interpreted by

Parrington (1946b, p. 186) as attachments for the *rectus capitis anticus* muscles. These depressions are relatively much deeper than those of larger specimens. In no. 42877, the left one has a foramen opening into its lateral wall, facing medially and a little posteriorly. This foramen opens into a canal, which disap-

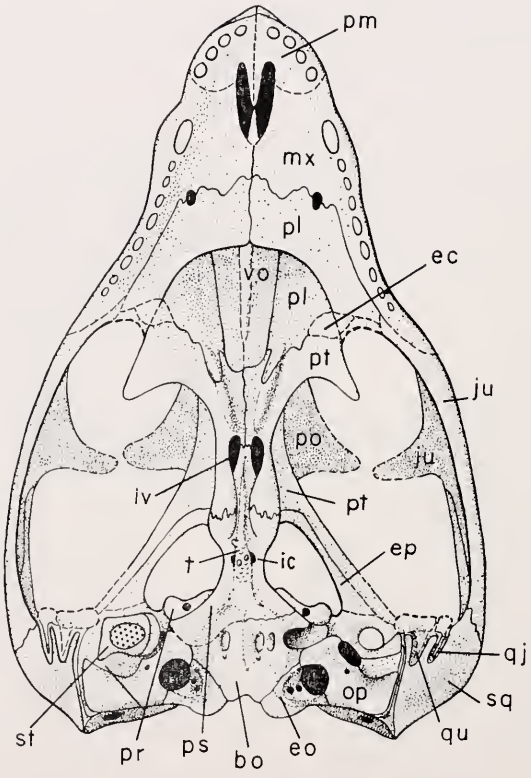

Fig. 2. Ventral view of restored juvenile skull of *Thrinaxodon liorhinus*; X about 2.5; for abbreviations see Fig. 1.

pears into the unossified area between the prootic and basioccipital. The foramen and its canal are formed wholly within the basioccipital. This is certainly the same structure as that described by Watson (1913, p. 220) in *Diademodon*, and is, as he suggests, probably venous. On the posterior slope of each muscle pit is a smaller foramen which is directed towards the occipital condyles. These are also visible in the adult (see Pl. 1, fig. 2).

In addition, a tiny foramen is present on the opisthotic about midway between the posterior borders of the jugular foramen and the fenestra ovalis.

Otic Region

The otic region is shown in detail in Figure 3B. Several additions may be made to Parrington's account of the fenestra ovalis region of *Thrinaxodon*. Of particular interest is the fact that he describes the fenestra ovalis as confluent with the "unossified region" (to be discussed below), which for the juveniles includes an area separating basioccipital from basisphenoid and prootic, except for a tiny contact with the latter at the anterior border of the cochlear recess (see below) in both adult and

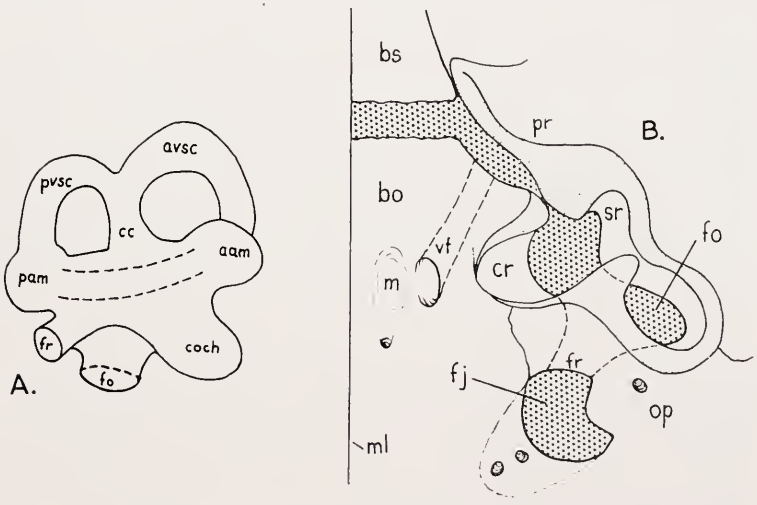

Fig. 3. A. Restoration of left inner ear of juvenile *Thrinaxodon liorhinus;* superointernal view, X about 7. Dotted line indicates position of horizontal semicircular canal.

B. Restoration of left otic region of juvenile *Thrinaxodon liorhinus;* ventral view, X about 7. The top of the figure is anterior. Parasphenoid omitted to show underlying structures. For abbreviations see Fig. 1.

juvenile. Figure 3B shows that in the juvenile, a process of the opisthotic almost completely closes the fenestra ovalis anteriorly; thus about three-fourths of the fenestral border is formed by the opisthotic, the remainder by prootic. A parasphenoid contribution to the fenestral border is small, if present, and the fenestra does not reach the basioccipital.

Posteriorly, the fenestra ovalis is confluent with the jugular foramen through a distinct channel, which lies entirely within the opisthotic and emerges within the jugular foramen near its external opening. It was apparently a complete canal in life, and must represent the fenestra rotunda. The presence of a fenestra rotunda was first demonstrated in therapsids by Simpson (1933, p. 289) in *Nythosaurus*. Olson (1944, p. 25) suggested that the perilymphatic duct in therapsids opens into the jugular foramen. These juvenile specimens demonstrate that this was the case in *Thrinaxodon liorhinus*, and that a fenestra rotunda was present in cynodonts more primitive than *Nythosaurus*.

Anterior to the fenestra ovalis, a deep recess is present in the skull base. It is formed principally in the basioccipital, except for its anterolateral and posterolateral corners, which consist of prootic and opisthotic, respectively. Apparently a thin cartilage coating was present on the interior of this recess, but its definite shape and relatively smooth inner surface indicate that it housed a soft structure and was not cartilage filled. The recesses were probably covered by parasphenoid in life, as in the adult, but breakage has now exposed them on no. 42877. The recess is partially roofed laterally by a small process of the prootic, which tends to separate it from the saccular recess (see below, and Fig. 3B). The recess in the basioccipital is present only as a slight concavity in the adult. In no. 42865 (a young adult in which the braincase was prepared by acid) the area is very slightly concave, but no distinct recess is present. The conformation of the fenestra ovalis is very similar, in the young adult, to that described by Parrington (1946). However, in no. 42865, the anterolateral notch, in the large opening described by Parrington as the fenestra ovalis, has a smooth, finished edge internally, and is confluent with the area immediately ventral to the anterior ampulla. This particular notch is probably the ventral edge of the saccular recess, while the recess in the basioccipital is certainly a receptacle for a cochlear apparatus. Relative reduction of the basioccipital recess in the adult is probably a result of early development of the ear region of vertebrates and very little increase in size as adult size is reached.

The jugular foramina are large, formed between the exoccipital and opisthotic, and on their concave posteromedial borders a pair of small foramina are present. These are confluent with the condylar canal, and carried the hypoglossal nerves.

The stapes is roughened and unfinished proximally, and evidently bore a heavy cartilage plug, fitting into the slightly bevelled sides of the fenestra ovalis. It was perhaps similar to

the ossified plug described by Parrington (1955, p. 14) in *Scylacops capensis*. Only about one-half of the articular end of the stapes covers the fenestra ovalis. The remainder projects into, and partly over, the opening into the so-called "unossified region" (Parrington, 1946b, p. 185) and thus comes near the lateral wall of the cochlear recess. The distal end of the stapes is unossified. There is a relatively large stapedial foramen, and the posterior limb of the stapes is slenderer than the anterior limb, the latter condition resembling that of the adult. The fenestra ovalis is separated from the "unossified region" by an anterior process of the opisthotic. Anteriorly, the vestibule of the fenestra ovalis is confluent with the cochlear and saccular recesses.

Restoration of the Inner Ear

A restoration of the inner ear of the juvenile (Fig. 3A) shows the position and relationships of the fenestra ovalis, cochlea, and fenestra rotunda. It is very similar to that figured by Olson (1944, fig. 10d) for the adult *Thrinaxodon*, differing chiefly in the relatively thicker semicircular canals, exit for the fenestra rotunda, and presence of the cochlea. So far as the bony canals are concerned, the ear structure is comparable with that figured by Simpson (1933, fig. 3) for late cynodonts, and later, for the monotreme *Tachyglossus* (Simpson, 1938, fig. 2).

Unossified Area of the Skull Base

The unossified area in the skull base of therapsids varies in extent in the various groups. Usually there is an unossified region between basioccipital and basisphenoid, and this may extend into the ear region. In *Thrinaxodon liorhinus* the contact between prootic and basioccipital-basisphenoid is mostly unossified in both adults and juveniles. There is almost a contact anteriorly between the prootic and basisphenoid in the juveniles (see Fig. 3B), but otherwise the area was cartilage filled. In the young adult skull mentioned above (no. 42865), the unossified gap between the basisphenoid and basioccipital is very small. From the prootic-basioccipital contact posteriorly, the side wall of the inner ear capsule of this specimen is unossified back as far as the fenestra ovalis. At this point the latter is separated from the unossified area by the process of the opisthotic mentioned above in the section on the otic region. This process is also present, though less discrete, in the fully mature skull discussed below.

Juvenile Characters of the Small Specimens

The restorations given in Figures 1 and 2 show that the two small specimens differ in few respects from adult *Thrinaxodon liorhinus*. The differences which do occur are probably the result of juvenility. These differences are discussed below.

The ossification is light, more so than might be expected in the adult of a smaller species. The bone is very cancellous and translucent.

All sutures are clearly visible. This is also often true of the adults, but the latter have well-knit, occasionally complex and inter-digitated sutures, while those of the small specimens are relatively more open and have less complication.

The presence of small interpterygoid vacuities can be explained by juvenility of the specimens. Presumably the pterygoid musculature was not yet well developed; in the adult, these muscles obliterate the vacuities by appression of the medial flanges of the pterygoids against the midline. In the adult specimen discussed below (see also Pl. 1, fig. 1), the former position of the interpterygoid vacuities shows as two slim grooves on each side of the midline.

The presence of parasphenoidal teeth in a therapsid is unexpected. Palatal teeth on pterygoids and palatines are found in gorgonopsians, as well as in other groups of mammal-like reptiles, and Vaughn (1958) has described sub-sphenoidal teeth in a small pelycosaur. These teeth may be more consistently present in therapsids than previously supposed. Perhaps they have passed unnoticed owing to removal by mechanical preparation, or obscured in the older individuals by appression of the pterygoids to the midline.

Differences in tooth number have been considered to be taxonomically significant, but individual variation between right and left sides in both juveniles and adults vitiates its utility. An example of ontogenetic variation is provided by the comparison of the greater number of juvenile than adult teeth in *Thrinaxodon liorhinus* with the converse situation in *Galesaurus planiceps* (Rigney, 1938, p. 512).

In animals which, as adults, possess well-developed sagittal crests, the lack of development of these crests in juveniles is a frequent phenomenon, both in reptiles and mammals. Thus, the weak temporal crests, relatively large parietal foramen, and flattened skull table between the temporal crests of these small specimens indicate their juvenility.

The principal difference between the University of California specimens and Brink's juvenile one (Brink 1955, p. 73) is in the degree of development of the anterior projections of the frontals. These spines, which thrust a wedge anteriorly between the nasals, are also found in *Glochinodontoides*, *Platycraniellus*, and *Galesaurus*. This is apparently a variable character in the juveniles of *Thrinaxodon liorhinus*, disappearing in the adults owing to further growth of nasals and frontals.

The other differences between adult and juvenile, pointed out by Brink, are present in the University of California specimens, though the presence of incomplete postorbital bars cannot be determined in this material. The relatively very large frontal of the juvenile is separated from the orbital margin by a very narrow meeting of the postorbital and postfrontal. The posterior margin of the secondary palate is at the level of the fifth tooth in the juvenile rather than the third as in the adult. The latter may be explained by the greater relative growth of the snout in the adult, and the greater number of anterior teeth in the juveniles.

THE ADULT SKULL

The specimen discussed here also came from the *Lystrosaurus* zone near Harrismith, and has been designated U. C. no. 40466. Plates 1 and 2 were prepared some years ago by Mr. Owen Poe, Staff Illustrator for the Museum of Paleontology, University of California. They are included here because no detailed figures of actual specimens of *T. liorhinus* have ever been published. The general anatomy of the adult *Thrinaxodon* skull has been elucidated by Parrington (1946b), and Olson (1944) has discussed the ear region, but this specimen shows some additional points of interest.

Foramina of the Snout

The maxilla bears a row of four to six large superior labial foramina along its ventral exterior surface. Other more dorsally placed foramina are more numerous, smaller, and open anteriorly, though some of the posterior ones are directed backwards. The anterior parts of the nasals also bear numerous similar foramina. Watson (1931, p. 1200) has suggested that in *Ericiolacerta* these foramina indicated either a mobile prolongation of the snout or highly developed sense organs such as a rhinarium or

vibrissae. Brink (1957a, p. 86) extends this interpretation to *Diademodon*, as does Attridge (1956, p. 67) for the therocephalian *Mirotenthes*. The broadly ancestral position of theriodonts to mammals may justify an interpretation of these foramina as indication of a rhinarium-like structure. It should be pointed out, however, that an equally vascular bone surface is present in some lizards. *Tupinambis* (Teiidae) shows near identity with *Thrinaxodon* in the shape, number, and distribution of these foramina. In addition, *Tupinambis* shows a dendritic pattern of vascular grooves emanating from many of the more dorsal maxillary foramina. These arborizations resemble those described by Brink (1957a) for *Diademodon*, though they trend dorsoposteriorly rather than anterodorsally as in Brink's specimen. *Tupinambis* also has an enlarged superior labial foramen, which opens forward on the maxillary surface near the posterior border of the external naris and is frequently continued into the latter by a shallow gutter. This condition duplicates that of *Ericiolacerta*, as described by Watson.

Van Valen (1960, p. 306) mentions this vascularization of the snout region in *Tupinambis*, but suggests that the foramina "from their positions and relative development to be mostly related to the development of the teeth." On the contrary, these external maxillary (superior labial and lateral ethmoidal) foramina of lizards transmit only nerves and blood vessels serving cutaneous structures. Dorsally, the foramina perforating the nasals and dorsal part of the nasal processes of the maxillae transmit cutaneous branches of the lateral ethmoidal nerve. These serve highly vascularized and richly innervated skin thickenings which surround the cartilaginous nasal tube (Oelrich, 1956, p. 88). All of the snout skin is firmly attached to the underlying bone, with the exception of the above-mentioned thickened area, which is slightly motile (*ibid.*, p. 87), though no more so than in any other lizard.

The labial foramina transmit cutaneous branches of the superior alveolar nerve and maxillary artery, both serving the skin of the lower snout and the lip (*ibid.*, pp. 62-63). The latter is very weakly developed in all lizards. Those branches of the maxillary artery and superior alveolar nerve which serve the teeth are transmitted through ventrally and internally opening foramina in the palatal shelf of the maxilla, and are completely separate from branches serving cutaneous structures.

The similarity of bone vascularization in *Thrinaxodon* and *Tupinambis* suggests, then, that these foramina in themselves may not be *sufficient* evidence to indicate the presence of associated extensive secretory, sensory, or muscular structures in *Thrinaxodon* or indeed in any other theriodont. Presence of numerous large foramina on the lower part of the maxilla near the alveolar border would, on the other hand, seem to preclude the presence of an extensive movable muscular cheek and lip. The vascular and nervous structures associated with these foramina would probably serve skin fairly closely united with the bone, for extensive movement of this skin would be disadvantageous. A muscular cheek, then, is probably to be correlated with the development of a posteriorly placed, single, external, infraorbital foramen as seen in mammals. So far as I am aware, no such structure, or even a tendency for such a grouping or codification of nervous and vascular snout structures is present in any theriodont.

In summary, this discussion does not suggest that rhinarium, hair, muscular cheeks and mobile lips were not present at all in some therapsids; rather, that at least some of the evidence which has been adduced for the presence of these or similar structures is necessarily inconclusive. An excellent summary of this evidence is given in Van Valen (1960).

Otic Region

The stapes of this adult specimen (no. 40466) was removed from the left side and cleaned, and the region of the fenestra ovalis carefully prepared (Pl. 2, figs. 2-5). The stapes resembles in a general way that described by Parrington (1955, p. 14, fig. 8) for *Scylacops capensis*. It consists of a round head, the posterior two-thirds of which fits over the fenestra ovalis. This head is concave, contrasting with the bevelled plug of *Scylacops* and also with the rounded head of the stapes of the juvenile *Thrinaxodon*. The head is continued ventrolaterally by two slender arms enclosing a large stapedial foramen, which opens dorsoventrally rather than anterolaterally as in *Scylacops*. The posterior arm is more slender, as in the juvenile. On the distal end of the bone a strong dorsal process curves posteriorly, so that the upper portion is visible ventrally. There is a smooth articulation with the quadrate rather than a pronounced boss as in *Scylacops*.

Temporal Musculature

Of special interest in this specimen are thin, bony sheets, present on both sides, and attached to the slightly thickened ventral border of the epipterygoid. These are visible in Plate 1, figures 1 and 2 as irregular sheets occluding the temporal vacuities. These sheets trend posteroventrally and are wrinkled and distorted. They are interpreted as ossified fasciae, and thus directly indicate attachment of a broad, muscular, aponeurosis. Ventrally on the right side, this ossified fascia approaches the posterior bones of the lower jaw near the anterior part of the angular. The broad posterior attachment of the fascia along the anteroposterior ventral edge of the epipterygoid excludes the possibility of the fascia reflecting the pterygoid musculature. It agrees, however, with Parrington's placement (1955, p. 22, fig. 11) of the temporal muscles, and probably reflects their lower attachment. These muscles probably inserted on the posterior bones of the lower jaw (perhaps in the fossa between the surangular and prearticular) as their homologue, the adductor externus group, does in *Sphenodon* and other reptiles.

SUMMARY

Two small skulls of *Thrinaxodon liorhinus*, a cynodont reptile from Lower Triassic Karroo beds of South Africa, show differences from large specimens which lead to interpretation of the former as juvenile. They provide the first record of parasphenoidal teeth in a therapsid, and demonstrate for the first time the presence of small interpterygoid vacuities in cynodonts. The otic region shows a fenestra ovalis almost wholly surrounded by prootic and opisthotic; a large recess in the basioccipital anterior to the fenestra ovalis probably housed a cochlea. A distinct channel connecting fenestra ovalis with jugular foramen is undoubtedly a fenestra rotunda. In a fully adult specimen, ossified fasciae give direct evidence of temporal muscle attachment. The presence of a highly vascularized maxilla in theriodonts is probably insufficient evidence in itself to indicate an extensive sensory or muscular cheek and snout region of mammalian type.

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I wish to thank the following people for numerous helpful suggestions and critical reading of the manuscript: C. L. Camp, Bryan Patterson, and J. T. Gregory. Special thanks must go

to Dr. H. B. S. Cooke for his advice and assistance in acetic acid and Glyptal techniques. I am also grateful to Dr. A. S. Brink for providing a sketch of the juvenile specimen described by him.

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PLATES

Plate 1

Fig. 1. *Thrinaxodon liorhinus*, adult specimen, dorsal view of U. C. no. 40466; X 1.5. Figure by Owen J. Poe.

Fig. 2. The same, ventral view.

Plate 2

Thrinaxodon liorhinus, adult specimen, U. C. no. 40466.

Fig. 1. Lateral view of skull, X 2. The lower border of the angular flange is restored from the opposite side. Figure by Owen J. Poe.

Fig. 2. Left stapes; internal view of footplate, X 5. The anterior surface of the specimen is towards the top of the figure.

Fig. 3. The same, ventral view. The anterior surface uppermost.

Fig. 4. The same, anterior view. The dorsal surface uppermost.

Fig. 5. The same, lateral view. The dorsal surface uppermost.

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TWO SYMPATRIC CUBAN ANOLES OF THE *CAROLINENSIS* GROUP

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No. 7 — *Two sympatric Cuban anoles of the carolinensis group*

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INTRODUCTION

The *carolinensis* group of the West Indian iguanid genus *Anolis* consists of forms sufficiently closely related that most or all of them have been considered subspecies of one species. The described forms occur both on the mainland of North America and on the Caribbean islands: *carolinensis* in the southeastern portion of the United States; *lerneri, brunneus, smaragdinus* on the Bahamas; *fairchildi* on Cay Sal; *longiceps* on Navassa; *maynardi* on Little Cayman; *porcatus* on Cuba; and *allisoni* on the Islas de la Bahia off the coast of Honduras and on Half Moon Cay off British Honduras. Only one representative of the group has ever been reported from any one locality. Thus it has always been assumed that *porcatus* was the single Cuban representative of the *carolinensis* group.

Some years ago an examination of the specimens under the name *Anolis porcatus* in the American Museum of Natural History and in the Museum of Comparative Zoology revealed a difference in the shape of the ear opening that initially was presumed to be a dimorphism: the ear opening was in one case circular (Fig. 3), and in the other markedly elongate (Fig. 2). Later, field work in Camaguey, Cuba, indicated that this was not a phenomenon of polymorphism in a single species but instead that two distinct species of the *carolinensis* group existed in central Cuba.

Dr. Richard Etheridge independently discovered the two conditions of the ear opening while studying the *carolinensis* group at the University of Michigan Museum of Zoology. He

called to our attention the apparent identity of the elongate-eared Cuban form with *Anolis allisoni* Barbour (1928) from Roatan Island off the coast of Honduras.

A direct comparison of the types of *A. allisoni* (M.C.Z. 26725, 26727-55) with specimens of both Cuban species in the Museum of Comparative Zoology confirmed Dr. Etheridge's observations. It was thus established that *Anolis allisoni* Barbour was an available name for one of the two Cuban forms. It was necessary, however, to determine the proper allocation of the much older name *Anolis porcatus* Gray 1840. We therefore provided Mr. J. C. Battersby of the British Museum (Natural History) with material to compare with Gray's types. He very kindly informed us that the name *porcatus* Gray applies to a round-eared form.

A. porcatus has been customarily considered as merely one of the subspecies of *carolinensis* (Barbour, 1937; Oliver, 1948). For the purposes of this paper and to facilitate discussion we refer to the Cuban round-eared form as *A. porcatus*. The subspecies of *carolinensis* have been described without any reference to the pronounced geographic variation found within *porcatus* in Cuba. Certainly the level of differentiation of some of the Bahaman subspecies could be duplicated within the Cuban populations of *porcatus*. However, subspeciation within *porcatus* and the relationship of the Cuban populations to the non-Cuban subspecies of *carolinensis* is a taxonomic problem that need not concern us here.

DEFINITION OF THE ANOLIS CAROLINENSIS GROUP

Long-snouted lizards having the nostril median to the canthal ridge and separated from the rostral by three scales (Fig. 1); a rostral that is bordered on the posterior dorsal margin by five scales; loreal rows usually 3-4; the anterior sublabials are wider than long, supradigital scales multicarinate; ventral scales at midbody in transverse and diagonal rows; ventrals and dorsals slightly keeled; dorsals and laterals subequal in size, smaller

than or equal to the ventrals; tail round in cross section. The body color is variable and changeable; it may be yellow, green, grey, blue, brown or variegated. There is pronounced sexual dimorphism. The males are larger, and are characterized by well-marked frontal and/or canthal ridges. The head scales are rugose; there is a reddish or mauve dewlap and enlarged postcloacal scales. In contrast, the females are smaller and lack the enlarged postcloacal scales; they also lack frontal ridges or elevated canthal ridges, the head scales are multicarinate, the dewlap is small.

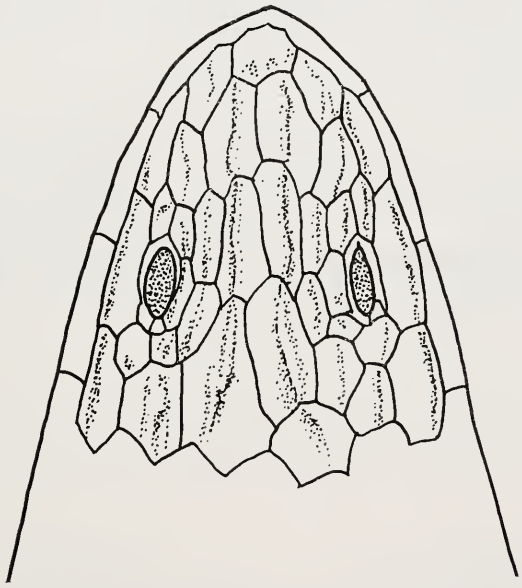


Figure 1. Dorsal view of the tip of the snout of a specimen of *A. porcatus* from Oriente. The *carolinensis* group characters of the rostral are shown: five scales bordering the rostral posteriorly and three scales between the rostral and nostril.

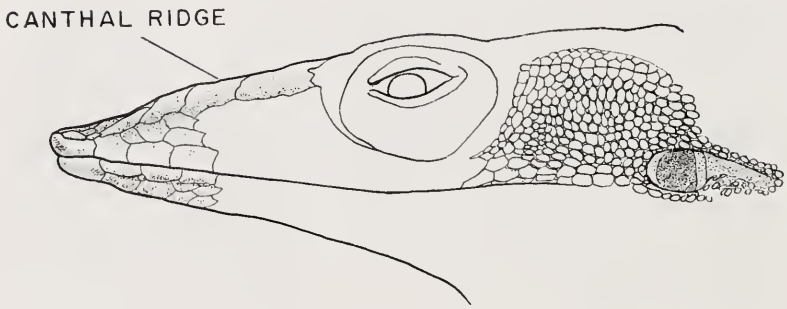


Figure 2. Head of a male *A. allisoni* from Camaguey. The elongate ear opening, the high canthal ridges, and the small postorbital scales are shown. The canthal ridges are so high that the frontal ridges are not visible in a lateral view.

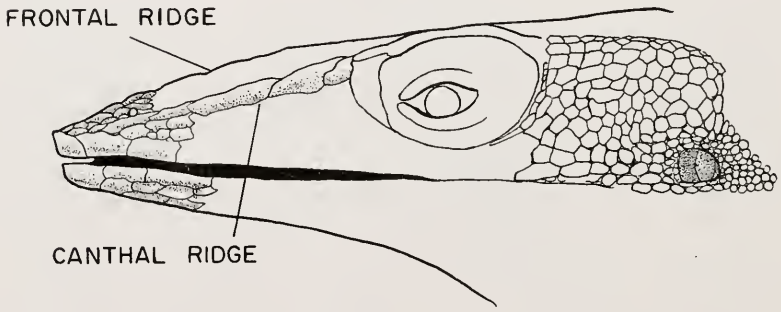


Figure 3. Head of a male *A. porcatus* from Camaguey. The circular ear opening, the high frontal ridges, and the large postorbital scales are shown.

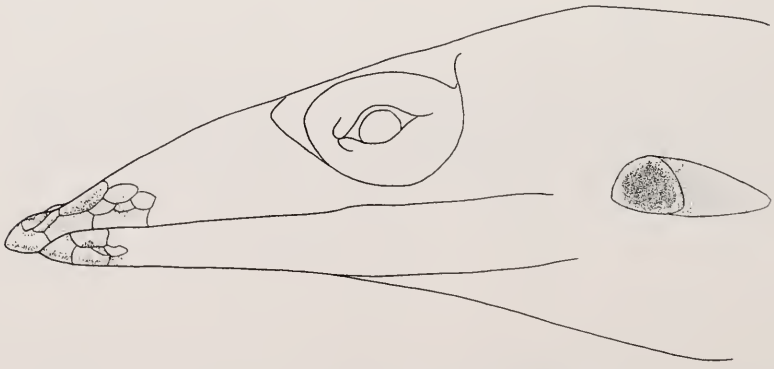


Figure 4. Head of a male *A. allisoni* from Roatan Island. The characteristic overlapping rostral scale of this population is shown.

COMPARISON OF ALLISONI AND PORCATUS

The following characters serve to distinguish *allisoni* from *porcatus*:

A. allisoni (Fig. 2)	*A. porcatus* (Fig. 3)
1. Ear opening is elongate, the posterior margin forming a long longitudinal depression.	1. Ear opening circular, or oval, the posterior margin not forming an elongate depression.
2. Temporal or postocular scales smaller.	2. Temporal or postocular scales larger.
3. Males with canthal ridges higher than the frontal ridges.	3. Males with the frontal ridges higher than the canthal ridges.

The elongate ear opening is a distinctive character of *allisoni* and is very different from the round or vertically oval ear opening of the other species of *Anolis*. In *allisoni* the tympanum resides in a depression having a sharply demarcated anterior margin formed by the temporal scales. Posterior to the tympanum is a triangular, elongate, scaleless groove that tapers posteriorly. Dorsally, the tympanum and groove are bounded by a loose fold of skin (Fig. 5).

In the entire genus *Anolis* the only examples that we have seen of an ear opening approximating this condition occur in some specimens of *porcatus* from Pinar del Rio, Cuba. In these specimens there is a short V-shaped posterior margin to the ear (Fig. 6). This condition in *porcatus* is not identical to the elongate depression in *allisoni*, but nevertheless does represent an approximation. About half of the 65 specimens examined of Pinar del Rio *porcatus* show some evidence of such a V-shaped posterior margin.

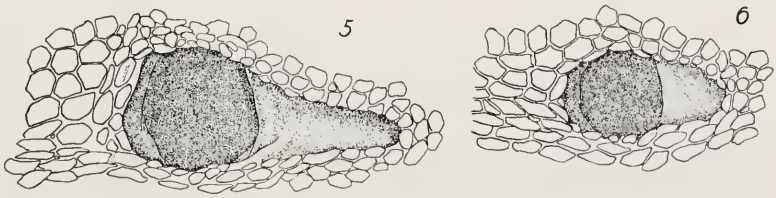


Figure 5. Ear opening of *A. allisoni* from Camaguey.

Figure 6. Ear opening of *A. porcatus* from Pinar del Rio. Some specimens of the allopatric populations of *porcatus* from extreme western Cuba show evidence of convergence toward *allisoni*, in having the posterior margin of the ear V-shaped and resembling the elongated posterior depression of the *allisoni* ear.

In life, the males of the two species are readily distinguishable since *allisoni* males have a brilliant blue head and thorax which is never seen in *porcatus* (Fig. 10). Gundlach (1880) in his discussion of *porcatus* mentions the blue form as a variant of *porcatus*. Similarly, Barbour and Ramsden in the "Herpetology of Cuba" (1919) confused the two species and provided a color description of *porcatus* that is a mingling of the characters of both species. They noted that the species (actually *allisoni*) was very common in the vicinity of Camaguey, and admit to having examined specimens from all six provinces.

The blue and green color of the *allisoni* males can change to an overall brown color. There is another transient color phase in which the green part of the body and limbs assumes a yellow color while the blue portion becomes a light violet color. The throat of the males usually shows some blue pigment, particularly in the area of the folded dewlap. A dark elongate spot is usually evident above the forelimb. The males also have a well-defined stripe from below the eye to the ear. The females of Cuban *allisoni* show no blue color and are solid green, and like the males can change to an overall brown. Living specimens of *allisoni* from the Cuban provinces of Las Villas, Oriente, and Camaguey do not differ in color or pattern. However, after preservation with formalin most of the Las Villas specimens show dark reticular markings over the nape and dorsum. These black reticular markings are present in life only during the brown color phase in the Camaguey specimens and are customarily not seen in the preserved animals.[1]

The blue color so distinctive of *allisoni* males is never present in *porcatus*.

VARIATION IN PORCATUS

A. porcatus shows pronounced geographic variation in color pattern (see Table 1). In the western portion of Cuba (Pinar del Rio and Habana provinces), *porcatus* can change in color from green to brown and shows a pattern of dark (black or dark green) reticulations over at least part of the body. There is also an elongate dark patch above the forelimb and single scattered white scales on the nape and parts of the body. Figure 7 shows

[1] We have seen two male *allisoni* which lacked the blue on the head and trunk. These animals were observed alive in the field (at the same locality) in Camaguey for a number of days. One of the specimens was collected and preserved (M.C.Z. 60928).

TABLE 1. Variations in the male specimens of *Anolis porcatus* in Cuba

"Eastern" *porcatus* (Oriente)	"Central" *porcatus* (Camaguey)	"Western" *porcatus* (Pinar del Rio)
1. Overall color green or brown. Very few variegations and with scattered white scales on the nape and body.	1. Overall color grey, light green, or brown. Variegated pattern and many white scales over entire body.	1. Overall color green, yellow-green or brown. Variegated dark markings and white scales on the nape.
2. Dark shoulder patch.	2. No shoulder patch.	2. Dark shoulder patch.
3. Males with a light vertebral stripe, bordered by a brown stripe on each side.	3. Males without a vertebral stripe.	3. Males without a vertebral stripe.
4. Round ear opening.	4. Round ear opening.	4. Round or partially elongate ear opening.
5. Low canthal ridges.	5. Low canthal ridges.	5. Very high canthal and frontal ridges.
6. Smaller, maximum size ♂ = 65 mm.	6. Smaller, maximum size, ♂ = 66 mm.	6. Larger, maximum size ♂ = 73 mm.

this type of pattern clearly. In the specimens from Oriente, at the extreme eastern end of the island, the color change ranges from green and grey-green to brown. There is a distinctive mid-dorsal light stripe bordered by darker pigment. The chin and throat area is well marked with longitudinal dark stripes. There is an ocellus (a spherical or elongate dark spot surrounded by white) above the forelimb. There is some evidence of reticular body markings on some specimens and often scattered white scales. Figure 8 is an illustration of an Oriente male of *porcatus*.

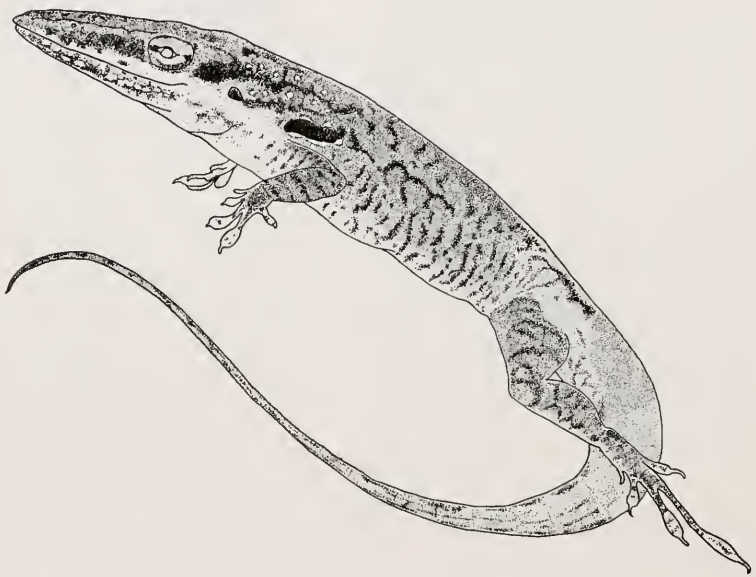


Figure 7. Male *A. porcatus* from Pinar del Rio. An example of a "western" *porcatus*.

In contrast to the eastern and western patterns the Camaguey populations of *porcatus* in the center of the island have an overall color of grey or light green or brown. The larger males are usually grey and some demonstrate no green color; however, females and some males do demonstrate a light green phase. Superimposed upon the grey color is a complicated pattern (Fig. 9) of dark and light reticulations. The body as well as the nape is covered with numerous white scales. The Camaguey

porcatus are thus sharply distinguishable from the sympatric and more abundant blue *allisoni*. The Camaguey specimens of *porcatus* are further distinguished by the absence of a white stripe below the eye which is characteristic and prominent in *allisoni*. However, it is interesting that Pinar del Rio *porcatus*

Figure 8. Dorsolateral view of a male *A. porcatus* from Guantanamo, Oriente. An example of an "eastern" *porcatus*.

show convergence to *allisoni* in having a white stripe below the eye similar to that of *allisoni*. Some of the other characters that readily distinguish the sympatric Camaguey *porcatus* from *allisoni* are not found outside the range of *allisoni*. The large flat temporals of Camaguey *porcatus*, which differ markedly from the small temporals of *allisoni*, are not so characteristic of the

Oriente *porcatus* where only the postoculars appear to be enlarged. Similarly some of the large males of *porcatus* from Pinar del Rio have canthal crests that are higher than the frontal crests and thus further resemble *allisoni* in this character. The specimens of *porcatus* from Las Villas (where *allisoni* is also found) seem to resemble the Pinar del Rio *porcatus* in the pattern of reticulations and in not being grey in color as is the Camaguey *porcatus*. However, we have only seen preserved Las Villas *porcatus* and therefore, do not know definitely whether the specimens from there ever assume a grey color. We have seen no live specimens from Matanzas province. The specimens of *porcatus* from Habana Province resemble the Pinar del Rio specimens.

The female specimens of *porcatus* do not demonstrate as pronounced a geographic variation as the males. The female

Figure 9. Male *A. porcatus* from Camaguey. An example of a "central" *porcatus*.

Camaguey *porcatus* usually show well-marked white scales on the lateral surfaces of the body and are thus readily distinguished from the eastern and western forms. The eastern females, like the males, show a middorsal light stripe bordered by a darker pigment. The females from western Cuba often show a brownish middorsal stripe similar, but not identical, to that of the eastern form. (Actually the middorsal stripe is a common characteristic of the female of many species of *Anolis*.) Even some female specimens of *allisoni* will at times have a narrow middorsal brown stripe that contrasts with the overall green.

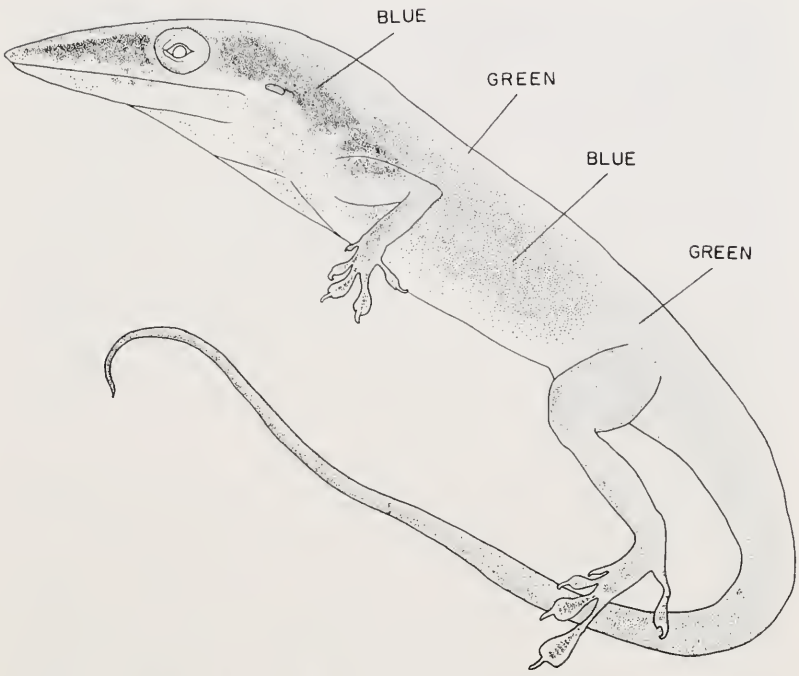


Figure 10. Male *A. allisoni* from Camaguey. The more heavily stippled areas on the head and thoracic region are blue while the rest of the body is green.

VARIATION IN ALLISONI

Anolis allisoni was originally described from Roatan Island by Barbour (1928) who recognized that it was closely related to *porcatus* and cited three scale characters by which it was supposed to differ from that species. Not one of these characters appears to be valid. His description of the male color pattern agrees with that given above for the Cuban *allisoni*. However, Barbour did not notice the peculiarity of the ear opening nor did he recognize that the Roatan *allisoni* was the same species that he had undoubtedly observed many times in Las Villas (at Soledad) and Camaguey. We have examined the types and paratypes in the Museum of Comparative Zoology, and a large series of specimens of *allisoni* from the Chicago Natural History Museum, and we can find only two characters that distinguish

the Islas de la Bahia specimens (from the Islands of Bonaca and Roatan) from the Cuban specimens of *allisoni*. In the Islas de la Bahia populations most of the males have an enlarged overlapping rostral (see Fig. 4). These specimens, when viewed ventrally, show a markedly projecting rostral that overhangs the tip of the lower jaw. Of a total of 34 male specimens with undamaged snouts, 24 (or 70%) had an overhanging rostral. In contrast, the rostral in the Cuban specimens is usually only slightly projecting. All of the Bonaca and Roatan specimens show dark reticular markings over the dorsum and nape, and also show white scales on the nape. This pattern resembles that seen in the brown phase of *allisoni* and also is much like the reticular pattern present on *porcatus* — from Pinar del Rio. In all other characters studied, the Cuban and Islas de la Bahia populations appear to be identical.

The distribution of *allisoni* is not limited to the Islas de la Bahia and Cuba. Specimens of *allisoni* have also been collected in Half Moon Cay (Schmidt, 1941), about 100 miles to the northwest of Roatan, near Turneffe Island (C.N.H.M. 30541 and 34628-9 and M.C.Z. 60983 — a total of 12 specimens). These specimens lack the overhanging rostral of the Islas de la Bahia forms. The color, in life, of the Half Moon Cay specimens is not known. As preserved, the specimens have irregular blotches of blue and purple and would thus appear to possess the blue pigment characteristic of the Cuban and Islas de la Bahia populations. The absence or presence of blue after preservation is, of course, not a definite indication of the true color in life. Unfortunately, the color of anoles is subject to unpredictable variation following death and preservation. Thus, the C.N.H.M. specimens from Bonaca and Roatan are all brown with dark reticulations and a single specimen from Half Moon Cay has the same pattern. However, Barbour's description of the Roatan populations does not mention such a pattern except as appearing after preservation. It is therefore possible that the reticulated pattern is made evident after preservation, and in life is only evident when the animal is in the brown color phase. The Half Moon Cay specimens, besides lacking an enlarged rostral, are also distinctive in that no dark shoulder patch is evident on any of the twelve specimens, that blue pigment is present on the ventral surface of the body, and that the white head stripe while evident below the orbit fades in the temporal area and is not visible posterior to the ear opening.

Morphologically, *allisoni* is thus divisible into three groups: Cuba, Islas de la Bahia, and Half Moon Cay.

CUBA	ISLAS DE LA BAHIA	HALF MOON CAY
1. Rostral slightly overlapping	1. Rostral strongly overlapping	1. Rostral not overlapping
2. Dark patch above forelimb	2. Same as Cuban population	2. No dark patch above forelimb
3. White stripe from ventral border of orbit to ear and some evidence of stripe posterior to the ear	3. Same as Cuban population	3. White stripe on ventral border of orbit, fading in temporal area, and not evident posterior to the ear
4. Belly color whitish	4. Same as Cuban population	4. Belly color possibly blue or green. Blue in preserved specimens, but color in life unknown
5. No white scales on nape	5. White scales on nape	5. No white scales on nape

It is immediately evident from the above that the Cuban and Islas de la Bahia populations are very similar while the Half Moon Cay population stands out as distinct from the other two. We believe that the morphological differentiation that has occurred in the Half Moon Cay and Islas de Bahia populations is evidence for assuming that these Central American populations of *allisoni* are old in these islands and not recent introductions by man. These three populations should probably be given subspecific designation to emphasize this fact. However, we have refrained from this step in the hope that we may be able to observe and compare living specimens of all three populations and thus confirm the color differences.

The differentiation of the Half Moon Cay and Islas de la Bahia populations is also evidence for assuming that the two populations represent separate invasions from Cuba. Thus, the Half Moon Cay population being the most differentiated can be considered to be the oldest or first invaders, while the Islas de la Bahia forms represent a more recent dispersal to the Central

American shore and thus more resemble the Cuban population. Certainly the differentiation of the two offshore populations preeludes our considering them as derived one from the other.

DISTRIBUTION

The round-eared form (or forms) which we are calling *A. porcatus* is found throughout the island of Cuba and on Isla de Pinos. At the western end of the island (Pinar del Rio and Habana) and at the eastern end (Oriente) it is the very common arboreal lizard found in well lighted areas around houses, in gardens, in pastures, in the edges of the forests, and probably in the forests in the higher sunnier portions of the trees. Next to *A. sagrei* it is the most common lizard on the island. However, in the provinces of Camaguey and Las Villas, *porcatus* is a rarer lizard. In this area *allisoni* is the common species, found in the identical habitats that *porcatus* occupies in the eastern and western portions of the island.

The abundance of *allisoni* in central Cuba, of *porcatus* in the eastern and western portions of the island, and of *sagrei* throughout the island is probably a recent phenomenon associated with the destruction of the forest and the introduction of agriculture. In a recent article (Ruibal, 1961) it was shown that *allisoni* and *sagrei* are ecologically restricted to open areas of high insolation. Both these species (and presumably *porcatus* as well) demonstrate a high temperature preference and bask in open exposed habitats. Previous to the destruction of the forests these species were probably restricted to the savannas, the open coastal vegetation (thickets), and similar sparsely covered areas. Using Waibel's (1943) estimates about the former plant life of Cuba, it appears reasonable to assume that probably 80 per cent of pre-Columbian Cuba was covered with broadleaf or hardwood forest. Currently only 11 per cent of the surface area of Cuba remains covered with broadleaf forests (Smith, 1954). *Allisoni, porcatus,* and *sagrei* thus represent species that originally were restricted in their distribution in Cuba, but with the destruction of the natural vegetation have spread and become the predominant anoles of the island.

Figure 11 shows that the range of *allisoni* is completely included within the range of *porcatus*. In Camaguey and Las

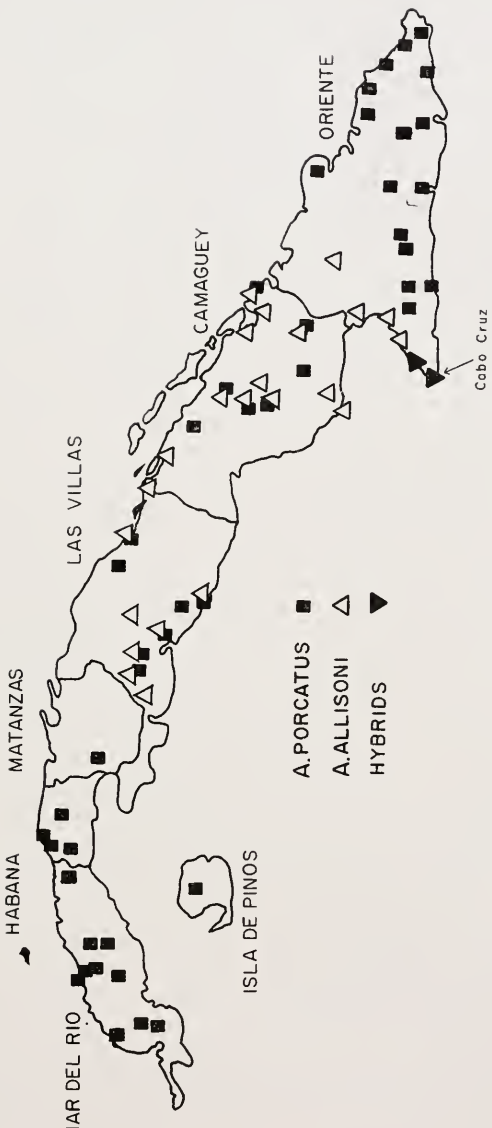


Figure 11. Map of the distribution of *A. allisoni* and *A. porcatus* in Cuba.

Villas the two species have not been collected together at all localities; however, wherever intensive collecting of *allisoni* has been done (Soledad, Trinidad, 9 km. west of Camaguey, and 15 km. southwest of Camaguey) specimens of *porcatus* have also been collected. Mr. Kevin W. Marx of the University of Minnesota observed these two species in the vicinity of Soledad, Las Villas, and was also impressed by the fact that the forms are sympatric and that *porcatus* was the rarer species (personal communication). Therefore, we believe that *porcatus* may be found throughout the range of *allisoni* but as a less common species. During field work in Camaguey in the summer of 1957 and 1959, only 12 specimens of *porcatus* were seen and collected while the number of *allisoni* seen was certainly in the hundreds — this, in spite of the fact that a purposeful search was made for *porcatus*. The males of the Camaguey *porcatus* are, of course, immediately recognized in the field due to their variegated pattern and white scales. The females are also recognizable but are not as brilliantly marked. *Allisoni* and *porcatus* in central Cuba are sympatric species. The exact ecological interrelationship of these two species is not known; nevertheless, the available evidence indicates that their respective ecological niches overlap. Both species have been collected in the same localities and in the same situations: on fence posts, on buildings, corrals, in banana groves, on palms (*Coccothrinax*) in coastal thickets, and along the edges of forests. In contrast *allisoni* has often been observed on the royal palm (*Roystonea*) and the coconut palm while we have never observed Camaguey *porcatus* on these palms. Similarly we have twice collected female *porcatus* inside the forest, and have never observed *allisoni* in such a habitat. In April of 1960 the senior author spent ten days in Camaguey and observed numerous specimens of *porcatus* on the trunks and branches of the "*algarrobas*" (*Samanea saman*) in a pasture near Camaguey. A diligent search was made for *allisoni* in this portion of the pasture and none was found. During these ten days in April more specimens of *porcatus* were observed than in the previous two summers of field work. It is thus possible that *allisoni* and *porcatus* may demonstrate some form of ecological temporal or seasonal replacement such as Neill and Allen (1959) have claimed for some lizards from British Honduras. However, the ecological data that we have obtained for *porcatus* in Camaguey has been of a fortuitous nature and thus prevents us from reaching any definite conclusions at this time.

The distribution of the two species has been plotted on the map in Figure 11 and the localities are listed at the end of the text. These localities are those represented by specimens examined from the collections of the Museum of Comparative Zoology, American Museum of Natural History, University of Michigan Museum of Zoology, United States National Museum, and the Chicago Natural History Museum. *A. allisoni* has so far been recorded from Las Villas, Camaguey, and the lowland western portion of Oriente. In contrast, *porcatus* is recorded from all of the six provinces and Isla de Pinos. In Oriente the distribution of *porcatus* is limited to the more mountainous areas and there is actually a distributional gap between the Oriente *porcatus* and the *porcatus* from Camaguey. This is a gap of about 150 kilometers between the easternmost Camaguey localities and the Oriente sites for *porcatus*. It is impossible at this time to determine whether this is an actual break in the range of *porcatus* or whether it merely reflects the lack of collecting in lowland western Oriente. Similarly only three specimens of *porcatus* all from one locality have been seen by us from Matanzas province. This is clearly the consequence of Matanzas being an area that has been singularly ignored by herpetological collectors. Future collecting in Matanzas should show *porcatus* to be as abundant as it is in Habana province.

Outside of Cuba, *allisoni* is found on Bonaca and Roatan in the Islas de la Bahia and at Half Moon Cay near Turneffe Island. It would appear probable that it is distributed throughout the other small islands in the Gulf of Honduras and it may possibly also be found in the neighboring mainland. *A. allisoni* thus has a disjunct distribution. The Little Caymans located part way between Cuba and the coast of Honduras are populated by *A. maynardi*, a form round-eared like *porcatus* and not close to *allisoni*.

The distribution of *allisoni* from central Cuba to the offshore islands of Honduras shows the most distant dispersal of any of the *carolinensis* group. It immediately raises the question of the evolutionary origin of *allisoni*. Any attempt to explain the zoogeography of *allisoni* and *porcatus* requires an analysis of the evolution and zoogeography of the entire *carolinensis* group. It would appear best to leave this aspect of the discussion to a later paper.

DISCUSSION

In all of the preceding discussion, the assumption has been that we are dealing with two species, one of which (*allisoni*) has a central distribution in Cuba while the second (*porcatus*) is represented by three geographic races spread along the entire length of the island. We made this assumption to facilitate the presentation of the data, and it is now necessary to critically examine the distribution and morphology of the Cuban forms and determine what other interpretations may be made of the data.

The variations described above for *allisoni* and *porcatus* permit us to distinguish, in Cuba, four morphological forms of the *carolinensis* group: *allisoni*, "western" *porcatus*, "central" *porcatus*, and "eastern" *porcatus*. Using these names now as simple labels without any taxonomic implications will allow us to analyze the distributional patterns. From the field observations in Camaguey and the morphology of *allisoni* and "central" *porcatus* it is obvious that these two sympatric forms are separate species. No morphological intermediates between *allisoni* and *porcatus* are known from Camaguey and Las Villas provinces. However, the relationship of these two central species to the eastern and western forms is not immediately apparent. At least the following four alternative interpretations (see Table 2) are possible:

Hypothesis 1. The "western" *porcatus* and *allisoni* are geographic races of one species, and the "central" and "eastern" *porcatus* are geographic races of another species. The main evidence in support of this hypothesis is that only in the "western" *porcatus* do we find an elongate ear opening approximating the external ear opening of *allisoni*. Furthermore, some of the large "western" *porcatus* males resemble *allisoni* in having a large canthal ridge. However, this hypothesis must assume a zone of morphological intergradation between the Pinar del Rio "western" *porcatus* and the *allisoni* from Las Villas and Camaguey. This hypothesis is untenable since the specimens from Habana and the few from Matanzas show no evidence of being morphologically intermediate between *allisoni* and *porcatus*. In addition, the "central" *porcatus* show a color pattern that closely resembles the variegated pattern of "western" *porcatus*. The hypothesis further assumes that the "central" and "eastern" *porcatus* are geographic races and should therefore

demonstrate morphological intermediates between the two races in Oriente. As mentioned previously, there is a distributional gap between the "central" *porcatus* in Camaguey and the "eastern" *porcatus* in Oriente (see Fig. 11). This gap may be more apparent than real; nevertheless, on present evidence it is a distributional hiatus.

Hypothesis 2. This is the reverse of the preceding hypothesis. In this instance, *allisoni* is considered to be a geographic race of "eastern" *porcatus* while the "central" and "western" *porcatus* would be geographic races of a second species. The similarity in ear and canthal ridges between *allisoni* and "western" *porcatus,* previously mentioned, would be interpreted as the result of convergence. Thus in central Cuba where the two species overlap they demonstrate pronounced divergence (*allisoni* as contrasted to "central" *porcatus*) while in the zones where a single species is to be found there appears to be morphological convergence ("eastern" and "western" *porcatus*). This interpretation would consider the *carolinensis* group in Cuba as an example of "character displacement" similar to previously cited cases of this type (Brown and Wilson, 1956). In support of this hypothesis it can be said that the patterns of the "central" and "western" *porcatus* are similar and can be easily imagined to be derived one from the other. The specimens of *porcatus* from Habana and Matanzas are variegated and do not present an obstacle to this interpretation as they do to the first hypothesis.

A further corollary of this hypothesis is that intermediate populations between *allisoni* and "eastern" *porcatus* should be found in Oriente. There is support for this from four male specimens (U.S.N.M. 138117, 138126-28) collected by Mr. Jerry D. Hardy, Jr., about 10 miles north of Cabo Cruz and at nearby Jucural. All specimens resemble *allisoni* but have the following *porcatus*-like characters:

1. A round ear opening in one specimen and the others with only a shallow groove posterior to the ear opening.

2. Two of the specimens show white spots on the nuchal area.

3. Three of the specimens demonstrate postoculars and temporals that appear to be intermediate in size between *allisoni* and *porcatus*.

However, a single female from the same area (U.S.N.M. 138125 from Jucural) shows no evidence of *porcatus* characters.

A series of 18 specimens from Cabo Cruz collected by Albert Schwartz also show evidence of hybridization between *allisoni* and "eastern" *porcatus*. Of the 11 males in the series only one shows a well developed ear depression while the others have poorly developed shallow areas posterior to the ear opening. These ears are morphologically very similar to some of the Pinar del Rio *porcatus* (Fig. 6). One male also has white spots on the nape. Four of the females have well developed *allisoni*-like ear openings. A single male (with an *allisoni* ear) shows a light middorsal stripe bordered by darker pigment like that of "eastern" *porcatus*.

The area of the hybrids (Fig. 11) lies where one would assume a zone of contact between *allisoni* and *porcatus; allisoni* is in the lowland western portions of Oriente while *porcatus* is in the more mountainous southern and eastern portions. *Porcatus* is found throughout the Sierra Maestra and would be expected to contact *allisoni* on the northern slopes and along the coastal area near Cabo Cruz. Collecting in this area indicates that the intermediate zone between *allisoni* and "eastern" *porcatus* must in any case be narrow — at San Ramon, 20 ml. northeast of this area "typical" *allisoni* have been collected.

Hypothesis 3. *Allisoni* is a species limited to the central portion of the island while *porcatus* is islandwide in its distribution. (The "eastern," "central" and "western" *porcatus* represent geographic races of the same species.) This, of course, is the way in which the data were presented preceding this section. We may now consider the evidence for and against this theory:

a) "Central" *porcatus* and *allisoni* are sympatric and do not interbreed. This fact at least establishes the distinctness of the two forms in Las Villas and Camaguey.

b) "Central" *porcatus,* though different from "eastern" and "western" *porcatus* in color pattern, shows many similarities to these two forms (structure of the ear opening, temporals, reticular markings, white scales, and low canthal ridges).

c) "Eastern" and "western" *porcatus* morphologically resemble each other more than either of them does *allisoni.*

Therefore, on morphological grounds alone it would be possible to consider "central" *porcatus* conspecific with the "eastern" and "western" forms. The "central" *porcatus* would still represent an example of character displacement where the

species is sympatric with *allisoni*. The "eastern" and "western" populations would in this case be considered to be connected across the length of Cuba by the rarer "central" *porcatus*.

This interpretation is weakened by the apparent distribution gap mentioned previously between "central" and "eastern" *porcatus*. The gap may or may not be real and all that we can do is hope that intensive collecting can be done in this area in the near future. It should be pointed out that a similar distributional gap exists in this area for *Anolis allogus* and *A. homolechis* (Ruibal and Williams, 1961). Furthermore, a comparable situation exists at the western end of the distribution of *allisoni*, in the province of Matanzas where very few records are available for any of the Cuban species of *Anolis*. Both the eastern and western distributional gaps may merely reflect the lack of herpetological collecting that has been done in these areas.

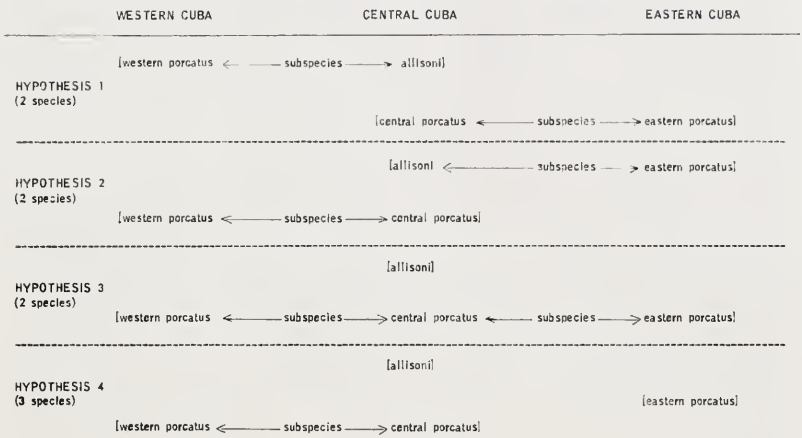
Also weakening this interpretation is the presence of hybrids in the area of Cabo Cruz, Oriente, between "eastern" *porcatus* and *allisoni*. However, the hybrids do not necessarily commit us to discarding this hypothesis. Sufficient cases are known in various animal species (Blair, 1941; Volpe, 1959; Gilliard, 1959) where hybrids occur when the ecological isolation between species has been disturbed. The evidence for intermediates between *allisoni* and "eastern" *porcatus* indicates that the zone of contact between the two morphological types must be narrow and that it corresponds to the border between the lowland agricultural areas and the less modified mountains. The Cabo Cruz area may represent a situation where the isolating mechanisms between the two species have broken down in an ecologically disturbed zone (i.e., where agriculture is actively encroaching into a forested area). It is of course also possible that a narrow zone of hybridization between *allisoni* and *porcatus* may exist throughout the periphery of the distribution of *allisoni*. In central Cuba the two species are presumed to have evolved mechanisms to reduce interspecific competition. The existence of character displacement and the fact that in the area of sympatry *porcatus* is less common and occupies a more restricted habitat than where it is allopatric to *allisoni* suggest that isolating mechanisms (behavioral, ecological, etc.) have evolved. However, at the periphery of the distribution of *allisoni* this species would be adjacent to populations of *porcatus* that have not been subjected to competition with *allisoni*. These populations of *porcatus* would be occupying the habitats

in which *allisoni* has proved superior (such as the arboreal habitat around houses and gardens). If these populations are brought into contact, by let us say a human disturbance of the habitat or by an expansion of one of the populations, an initial hybridization between the species is not unreasonable. With time, selection would operate so that each species would be segregated in the ecological niche to which it was best adapted and the hybrids would be eliminated. This of course presupposes that the hybrids are not as successful or well adapted as the parental species. Unfortunately, we have no data concerning the viability of the hybrids from Cabo Cruz or the precise ecology of this area.

Hypothesis 4. The final hypothesis to be considered is a three-species one (see Table 2). In this case *allisoni* and the "eastern" *porcatus* would be two separate species while the "western" and "central" *porcatus* would constitute a third species. This assumes that the distributional gap in Oriente between "central" *porcatus* and "eastern" *porcatus* is a real one or at least not occupied by populations morphologically intermediate between "central" and "eastern" *porcatus*. It would also assume that the hybrids between *allisoni* and "eastern" *porcatus* are explainable in the same manner as for the previous hypothesis.

Three of these hypotheses can be discarded if collecting in the distributional gap between "central" and "eastern" *porcatus* yields specimens that are morphological intermediates between these two forms. The only hypothesis that would be retained would then be the third case presented — *allisoni* as a centrally distributed species with *porcatus* represented by three geographical races, "eastern," "central" and "western." If no intermediates are found in this zone then a more detailed analysis of the zone of contact between *allisoni* and *porcatus* in Oriente will be mandatory.

TABLE 2. Diagram of the four hypotheses that are considered applicable to the data presented on A. allisoni and A. porcatus.



SUMMARY

1. The *carolinensis* group of *Anolis* is defined and two closely related Cuban representatives of the group, *porcatus* and *allisoni* are described.

2. *A. allisoni* is found in central Cuba (Las Villas, Camaguey, and western Oriente) and is sympatric with *porcatus* in this area. *A. porcatus* is apparently island-wide in its distribution and is a common species in eastern and westernmost Cuba, but it is rare in central Cuba.

3. *A. allisoni* is also found on a number of islands off the Central American mainland. Evidence is presented that indicates that *allisoni* is not a recent introduction by man into these offshore islands.

4. On Cuba, *allisoni* and *porcatus* show evidence of character displacement and convergence.

5. Both species on Cuba are considered examples of species that were preadapted to occupy the areas cleared of forest and modified by man's activities.

6. Three morphological forms of *porcatus* are described in Cuba, "western" *porcatus*, a "central" *porcatus*, and an "eastern" *porcatus*.

7. Evidence of hybridization between *allisoni* and "eastern" *porcatus* is presented.

8. Four hypotheses are presented to explain the distribution and biology of the three forms of *porcatus* and of *allisoni*.

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LOCALITY LIST

Hybrids

CUBA

Oriente: Cabo Cruz; 10 ml. N. of Cabo Cruz; Jucural (between Cabo Cruz and Niquero).

A. porcatus

CUBA

Pinar del Rio: San Diego de los Baños; Viñales; Guane; Pinar del Rio; San Vicente; just N. of San Vicente; near Isabel Rubio; Cayo la Reina near Puerto Esperanza; nr. Herradura; Guanajay; Dimas.

Habana: Habana; Regla; San Antonio de los Baños; San Jose de las Lajas; Isla de Pinos.

Matanzas: Alacranes (Alfonso XII).

Las Villas: Rodas; Baños de Ciego Montero; Soledad; Central Purio; Caibarien; Sierra de Trinidad; Trinidad; Cienfuegos.

Camaguey: Marti; 9 km. W. of Camaguey; 15 km. S.W. of Camaguey; Playa Sta. Lucia (E. of the Bahia de Nuevitas); Sierra de Cubitas; Sierra de Najasa; Loma de Cunagua.

Oriente: Santiago; Jiguani; Upper Rio Ovando; Coast S. of Pico Turquino; Pico Turquino: Imias; Banes; Baracoa; Guantanamo: Buey Arriba; Sagua de Tanamo; Moa; Miranda; 27 km. S. of Yara; mouth of Rio Yumuri; Cananova; Calabazar; Bayate.

A. allisoni

CUBA

Las Villas: San Isabel de la Lajas; Baños de Ciego Montero: Trinidad; Soledad; Caibarien; Central Covadonga; Rodas; San Jose del Lago; Central Caracas.

Camaguey: Camaguey; Marti; Cascorro; 15 km. S.W. of Camaguey; Playa Sta. Lucia (E. of the Bahia de Nuevitas); 13-20 km. S. of Playa Sta. Lucia; 7 km. N.E. of Sta. Cruz del Sur; Sta. Cruz del Sur; 9 km. W. of Camaguey; Bahia de Nuevitas; Moron; Banao; Tana.

Oriente: Birama; Omaja; San Ramon; 5 ml. S.W. of Manzanillo.

HONDURAS

Islas de la Bahia: Roatan; Bonaca.

BRITISH HONDURAS

Half Moon Cay

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THE TAXONOMY OF THE *ANOLIS HOMOLECHIS* COMPLEX OF CUBA

By

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CAMBRIDGE, MASS., U.S.A.
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No. 8 — *The Taxonomy of the Anolis homolechis Complex of Cuba*

By Rodolfo Ruibal and Ernest E. Williams

INTRODUCTION

In Barbour and Ramsden's (1919) "Herpetology of Cuba" nineteen species of the genus *Anolis* were recognized. Of these, five were grouped together as related, in both the key to the species and in the text. These species are: *A. homolechis* (Cope) 1864, *A. mestrei* Barbour and Ramsden 1916, *A. rubribarbus* Barbour and Ramsden 1919, *A. quadriocellifer* Barbour and Ramsden 1919, and *A. allogus* Barbour and Ramsden 1919. Later, two more species were described that were related to this group: *A. ahli* Barbour 1925, and *A. patricius* Barbour 1929. In 1937 Barbour published the "Third list of Antillean reptiles and amphibians." At this time he further emphasized the interrelation of the various species in the group by making trinomials of all names, as follows:

A. allogus allogus
A. allogus mestrei
A. allogus ahli
A. homolechis homolechis
A. homolechis rubribarbus
A. homolechis quadriocellifer
A. homolechis patricius

It must be pointed out that *A. mestrei* was described in 1916, three years before *A. allogus*. Consequently, the trinomials involving these two names are incorrect as a matter of nomenclature. Furthermore, a careful analysis of the morphology of these six described forms indicates that Barbour was also wrong in regard to the species and subspecies groupings of the various forms.

In the sections that follow an attempt is made to redescribe the forms on a sound morphological basis and to determine the interrelationship of the various species. The data for this work have been obtained by a study of the types of five of the six described forms (only the type of *homolechis* was not seen), and the specimens of these species in the Museum of Comparative

Zoology and the American Museum of Natural History, as well as the paratypes of *A. mestrei* from the United States National Museum in Washington. Further information was obtained during six weeks of field work in 1957 in the Province of Camaguey, Cuba, as well as ten weeks of field work in 1959 in Camaguey, Oriente, Las Villas, and Pinar del Rio.

THE *HOMOLECHIS* GROUP

All of the named forms here discussed can be distinguished from the other Cuban species of *Anolis* by the following complex of characters: Head scales usually keeled, with a single median keel or with two or more keels; ventral scales smooth, with a convex posterior border, and in diagonal and/or longitudinal rows; dorsals small, non-imbricate, smooth or keeled, the middorsal scales slightly larger but grading in size imperceptibly to the smaller laterals; tail laterally compressed. Frontal ridges and a sharp canthus rostralis. Marked sexual dimorphism. The females are smaller, have multikeeled head scales, the dewlap is absent or very small, and they have a different color pattern. The males are larger, have usually a single keel to the head scales, have a large dewlap, and often have a well-developed fin to the tail.

The species of this group are all forest-dwelling forms. They are customarily to be found in shaded areas but some occur in the sunnier margins of the forest.

CHARACTERS

Preserved specimens of the various species that compose the *homolechis* complex are not readily distinguishable. Scale characters can be used to separate most of the species; however, all of the scale characters are subject to considerable variation. In the field, color and pattern differences allow immediate and absolute identification of the species but these are usually destroyed or obliterated during the fixation and preservation of the animals. In the field also, the species distinctions are made more evident by the ecological separation observable between the various forms. The unravelling of the various described species in this complex has been possible only because the field work in Cuba allowed us to observe the lizards while alive.

The most useful diagnostic characters are listed and defined below:[1]

1. The number of scales that separate the supraorbital semicircles. There may be from 0-3 scales between the semicircles.

2. The type of suture between the mentals and the small postmental scales. This may be a transverse suture (Figure 6b) or the small postmentals may separate the posterior medial margins of the mentals (Figure 6a).

3. The structure of the supracarpal and supradigital scales. These scales may be smooth, have a single keel, or be multicarinate and mucronate (Figure 7).

4. The number of scales between the first canthals. This may vary from 4-12 scales. The first canthal is defined as the anteriormost enlarged and elongate canthal scale.

5. The structure of the scale anterior to the external naris. This scale may be single or divided by a median horizontal suture (Figure 8).

6. The size of the scales along the posterior border of the interparietal. These scales may be large and sharply distinguishable from the dorsals (Figure 3) or they may be small and grade into the dorsals (Figure 4).

7. The head/ear ratio as an indication of the size of the ear. The head length is measured with Vernier calipers and is the distance from the tip of the snout to the anterior border of the ear

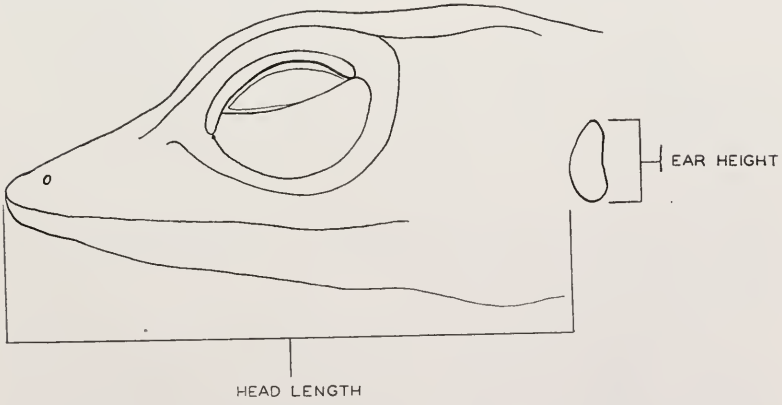

Figure 1. The head length and ear height measurements. These distances are best measured with the use of calipers.

[1] The scale terminology used is that defined by Smith (1946).

opening (Figure 1). The ear height is measured with the calipers and is the maximum distance from the ventral to the dorsal edge of the ear opening (Figure 1).

8. The body/femoral ratio as an indication of the length of the hind limbs. The body length is the snout-vent length measured with a ruler and is the distance from the tip of the snout to the vent. The femoral length is taken with a ruler and with the femoral region perpendicular to the body, and is the distance from the midventral line (pubic symphysis) to the knee (Figure 2).

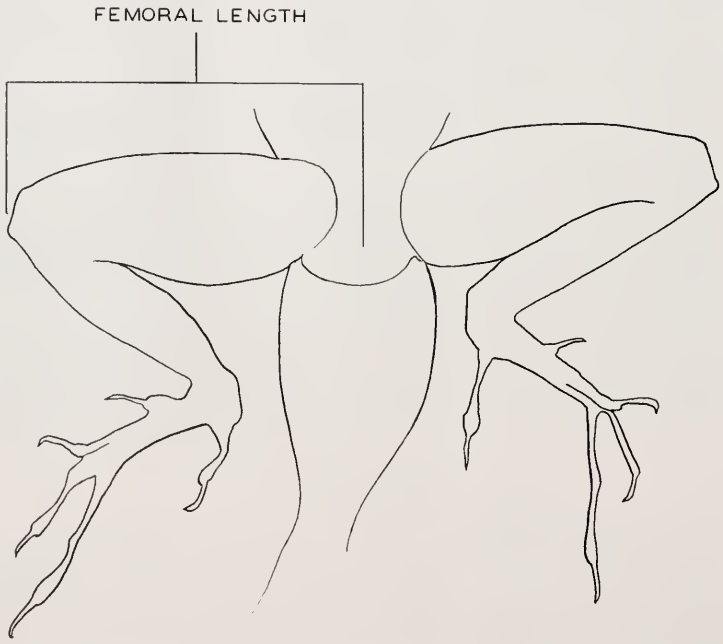

Figure 2. The femoral length measurement. The midventral point of reference is the pubic symphysis.

9. The color and pattern of the animal. The dewlap color and pattern easily distinguish the species in the field but these striking differences usually disappear or are little evident in preserved specimens. The body color and pattern are also very useful in the field; these are sometimes still evident in preserved specimens.

THE SPECIES

A definition of each of the species is provided below as well as general comments on the taxonomy, distribution, and ecology of the forms. Unless there is a statement to the contrary, all descriptions and comments are based exclusively on male specimens. In general the females of the various species can be distinguished by the same scale characters that distinguish the males, and differ also in the color pattern of the body. Except in one case all color descriptions in this paper are based on live specimens.

With the exception of *ahli*, all the species of the *homolechis* group may have high caudal fins in the males. This, however, is a variable character and often, within a single population, some males are devoid of a caudal crest while others have the crest well developed. The few (12) males of *ahli* that we have seen lacked a caudal fin.

The list of the localities for the species is given at the end of the text. The data were obtained from the specimens in the American Museum of Natural History, the Museum of Comparative Zoology, and the United States National Museum.

Anolis allogus Barbour and Ramsden

A. allogus Barbour and Ramsden, 1919.
A. allogus allogus, Barbour, 1937.
A. abatus Ahl, 1924.

Type locality. Bueycito, S. of Bayamo, Oriente, Cuba.

Definition. Supraorbital semicircles separated by two scales (Figures 4 and 9); a transverse suture between the mental and postmentals (Figure 6b); supracarpal and supradigital scales multicarinate and mucronate (Figure 7b); usually with 7-9 scales between the first canthals (Figure 10); scale anterior to the naris divided by a horizontal suture (Figure 8); scales around the posterior margin of the interparietal small and grading into dorsals (Figure 4). The body/femoral ratio averaging 3.3 (Table 1); the head/ear ratio averaging 6.2 (Table 2). Maximum snout-to-vent length: ♂, 58 mm., ♀, 41 mm.

Body color of ♂ ♂ in life with reddish and yellow reticulations. Color may change from a pale pink or tan to a very dark red-brown. Yellow reticulations usually prominent when in dark color phase. Tail is usually redder than the body. Iris metallic blue or grey. Usually some evidence of four dark

chevrons on dorsum. Dewlap ground color ranging from light yellow to apricot with 3-4 reddish stripes and a white margin (Figure 11).

The females have a wide middorsal light stripe (tan or yellow in color) while the dorso-lateral areas are a darker brown color. The middorsal stripe may have a scalloped margin and in a few specimens evidence of diamond-like markings in the light stripe may be seen.

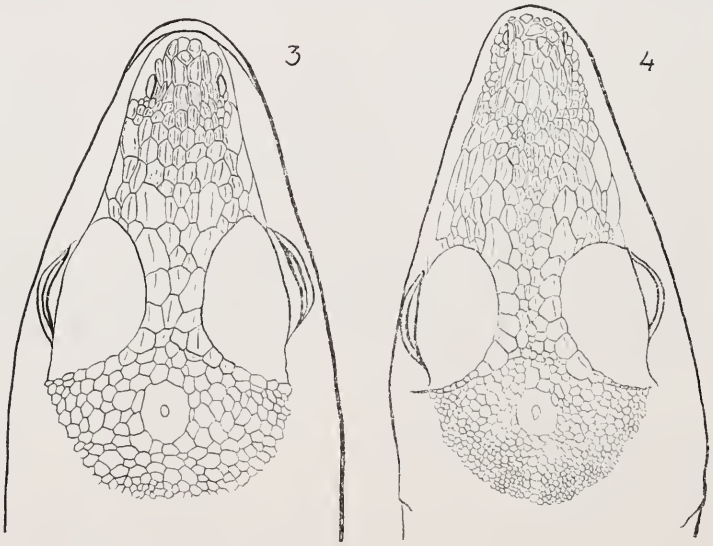

Figure 3. Dorsal view of the head of *Anolis homolechis.*
Figure 4. Dorsal view of the head of *Anolis allogus.*

Taxonomy. We have examined the type specimen of *Anolis abatus* Ahl and regard it as synonymous with *allogus.*

Our description of *allogus* differs from the color description provided by Barbour and Ramsden. They describe the body color as brown to black and the dewlap as yellow with a carmine spot. To resolve this discrepancy a collecting trip was undertaken to the type locality in the northern foothills of the Sierra Maestra. There is no longer any forest in the vicinity of Bueycito and it was necessary to travel farther into the foothills to Buey Arriba (8 km. south of Bueycito) to find forest and collect the species. The specimens from Buey Arriba have a yellow-tan

dewlap with three bright red stripes, and the body color is reddish as described above for the species. We feel that the color description of Barbour and Ramsden is probably erroneous. The red stripes in *allogus* are not sharply demarcated and

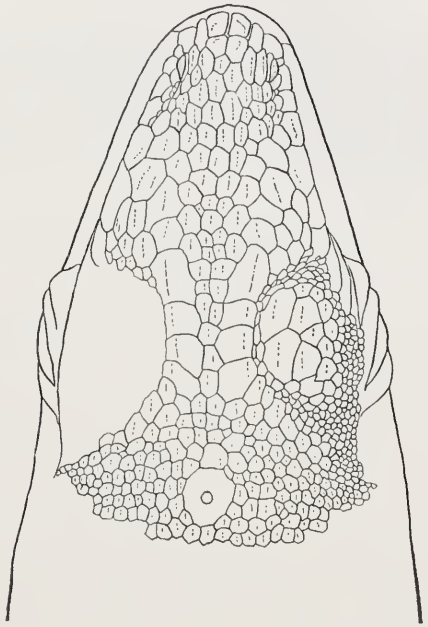

Figure 5. Dorsal view of the head of *Anolis mestrei*.

Figure 6. Ventral view of the chin showing the diagnostic postmental scales. (a) *A. homolechis;* (b) *A. allogus.*

often are very near to each other. In alcoholic specimens the three or four separate stripes often appear confluent. In all other respects the type specimen and the other specimens that Barbour ascribed to *allogus* are in agreement with our description.

Distribution. This species is recorded from all of the provinces except Matanzas and Las Villas; it is also absent from the Isla de Pinos (see Figure 13). The lack of records from Matanzas and from the portion of Las Villas outside the Sierra de Trinidad may be the consequence of insufficient collecting in these areas, or agriculture may have destroyed the natural habitat of the species.

Variation. There is no evidence of any significant geographic variation. The color and pattern of the dewlap is variable (see Figure 11) but we do not consider the variants well enough defined to merit taxonomic recognition. At Buey Arriba in Oriente the two or three red stripes are bright red, while in many of the Camaguey specimens the stripes are often very faint and of an orange color. Specimens may show from two to four stripes. In Pinar del Rio the background color is apricot while in most of the other localities it is best described as yellowish or tan.

Some of the specimens from Oriente Province (Baracoa, coast south of Pico Turquino, mountains north of Imias) though not distinguishable from *allogus* by any scale characters, show a general pigmentation pattern that differs from that of other Oriente *allogus*. As preserved, these specimens are devoid of a body pattern and show a pale body coloration (tan) and a dark dewlap. It is, of course, not improbable that the mountainous areas of Oriente will prove to have forms related to *allogus* that are distinguishable only by the dewlap or body color (as are *ahli* and *rubribarbus*). Isolation of populations in the various valleys and ranges of Oriente would permit the evolution of distinct forms. However, the detection and recognition of such forms requires detailed data from the living animals.

Ecology. The ecology of this species is discussed in some detail in Ruibal (1961). It is a forest-dwelling species restricted to the cooler, deeply-shaded portions of the broadleaf forests, perching on small tree trunks a few feet from the ground. Characteristically not a shy species, it will usually allow the collector to approach within a foot before escaping by running down to the base of the trunk or to the ground.

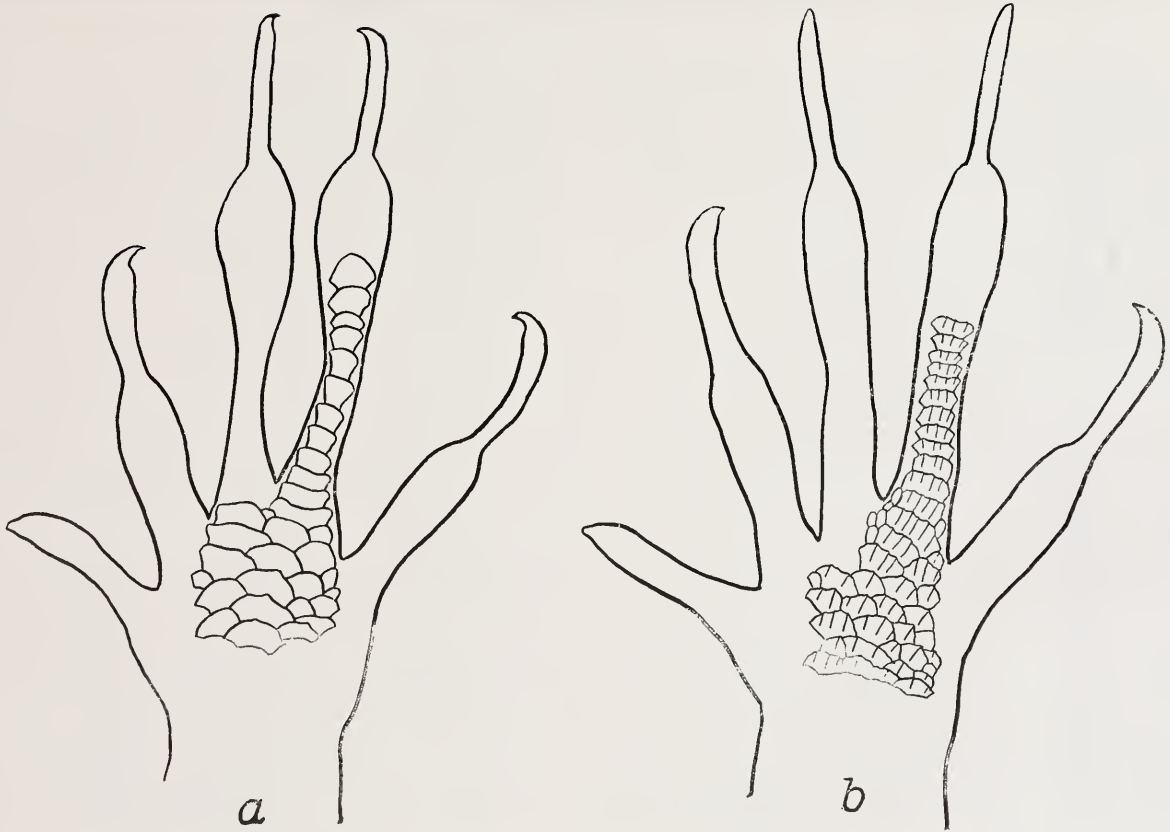

Figure 7. The supracarpal and supradigital scales of (a) *A. homolechis* and (b) *A. allogus*.

TABLE 1. THE BODY/FEMORAL RATIO OF THE SIX SPECIES

The values for *homolechis* and *allogus* include samples from Pinar del Rio, Camaguey and Oriente. The range for each species is in parentheses below the mean.

Species	*N*	*Mean*	σ	σM
homolechis	169	3.6 (3.1–4.0)	.16	.01
allogus	96	3.3 (3.0–3.8)	.21	.02
ahli	11	3.3 (3.0–3.6)	.16	.05
rubribarbus	17	3.3 (2.7–3.6)	.15	.04
mestrei	24	3.2 (2.9–3.5)	.15	.03
imias	1	3.1	—	—

TABLE 2. THE HEAD/EAR RATIO OF THE SIX SPECIES

The values for *homolechis* and *allogus* include samples from Pinar del Rio, Camaguey and Oriente. The range for each species is in parentheses below the mean.

Species	*N*	*Mean*	σ	σM
homolechis	162	7.7 (6.0–9.7)	.45	.04
allogus	100	6.2 (4.9–8.2)	.70	.10
ahli	12	6.3 (5.7–6.8)	.38	.11
rubribarbus	17	7.6 (6.3–8.6)	.75	.18
mestrei	20	8.5 (6.2–9.7)	.87	.20
imias	1	6.0	—	—

The females appear to be more terrestrial than the males, and are often found in the leaf litter on the floor of the forest and at the base of the small trees.

This species is absent from the coastal forests, savannas, pine forests, and from agricultural areas. We have never observed it near human habitations or in gardens.

Previous to the destruction of the Cuban forest, *allogus* was probably a widespread and common species. With the destruction of its natural habitat this species is now restricted to the small patches of dense forest that remain on the island. It has been collected at many localities in the Sierra Maestra and as high as 4000-6000 feet on Loma Cordero near Pico Turquino.

The apparent absence of *allogus* from the Isla de Pinos (where *homolechis* is found) may be the result of the specialized ecological requirements of this species for deeply-shaded, cool forests. The forests of Isla de Pinos may not be dense enough to provide this type of habitat. Furthermore, over-water invasion of the Isla de Pinos is hampered by the low thermal tolerance of *allogus*.

Anolis ahli Barbour

A. ahli Barbour, 1925.
A. allogus ahli, Barbour, 1937.

Definition. The scalation of this species cannot be distinguished from that of *A. allogus*. The body/femoral ratio and head/ear ratios are also identical to *allogus* (see Tables 1 and 2). The maximum snout-to-vent length: ♂, 58 mm. and ♀, 43 mm.

The body color of this species usually shows a greenish cast and the general color may shift from tan to dark brown. A common body pattern is a "salt and pepper" speckling. Usually four dark saddle markings are visible on the dorsum. The iris is blue. The dewlap has a large red spot that is surrounded by a yellow-white area (Figure 11).

Taxonomy. In the 1937 checklist, Barbour placed this form under *allogus* as a subspecies. The two forms are allopatric; the nearest recorded locality for *allogus* is at the Loma de Cunagua in western Camaguey. We have been conservative in utilizing the trinomial and prefer to view *ahli* as a full species. The lack of scale character differences between *ahli* and *allogus* does not prevent their being considered full species: the body

color and dewlap color pattern sharply distinguish the two forms. Color patterns are certainly as "important" as scalation in distinguishing species.

Distribution. This species is known only from the Sierra de Trinidad in Las Villas.

Ecology. This species has been collected in the darkest, shaded parts of the forest in the Sierra de Trinidad. It perches a few feet from the ground on tree trunks. It is a shy species and usually will run to the base of the trunk or to the ground on the approach of a collector. It is often difficult to distinguish the lizards from the background in the dim light of the forest. It appears to be the ecological equivalent of *allogus* in the Sierra de Trinidad.

Hardy (1958) has described the use of the tail by this species as a prehensile organ. We have observed that all of the species of the *homolechis* complex can curl the tail laterally into a tight whorl. We have, however, failed to observe any actual prehensile use of the tail. As mentioned previously, this species is the only one of the *homolechis* group in which no males have been observed with well developed caudal crests.

Anolis rubribarbus Barbour and Ramsden

A. rubribarbus Barbour and Ramsden, 1919.
A. homolechis rubribarbus, Barbour, 1937.

Type locality. Puerto de Cananova; near Sagua de Tanamo, Oriente, Cuba.

Definition. The scalation of this species is the same as that of *allogus* except for the structure of the scale anterior to the naris. In most specimens of *rubribarbus* this is a single scale that extends from the margin of the nares to the rostral (Figure 8).

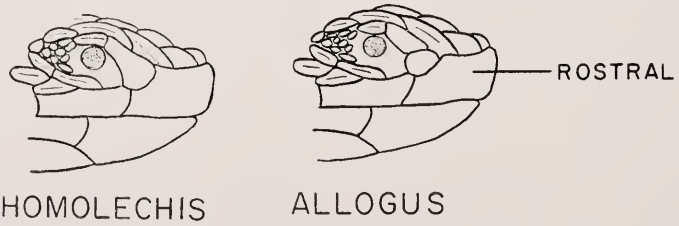

Figure 8. The structure of the scale anterior to the external naris in *A. homolechis* and *A. allogus.* In *A. rubribarbus* the scale is usually single as in *A. homolechis.*

In *allogus* and *ahli* this scale is divided by a horizontal suture. The body/femoral ratio averages 3.3 and is identical to that of *allogus* (Table 1). The ear is smaller than that of *allogus* or *ahli* and the head/ear ratio average is 7.6, very close to that of *homolechis* (Table 2). The maximum snout-to-vent length: ♂, 62 mm., ♀, 42 mm.

The general body color of this species is usually grey. It ranges from a pale grey to an almost black ground color. Yellow spots and reticulations may be present on the sides. The body may show no pattern with only a pale grey color or a "salt and pepper" marking. However, the most characteristic color phase is a pattern of dark (blackish) vertical bands separated by lighter (yellowish or grey) bands (see Figure 14). In this phase there are about six vertical bands on the body and more on the tail. The limbs are also banded. The dark body bands are usually narrower in the middorsal area and widen laterally, while the lighter bands show the reverse. The iris is blue-grey. This species has the most brilliant and distinctive dewlap pattern of any of the Cuban anoles (Figure 11) — 4-5 thin red stripes on a deep yellow ground. The scales along the edge of the dewlap are large and white and provide a white margin to the dewlap. The scales on the inner portions of the dewlap are smaller and black. The chin has well-marked dark reticular markings.

We have no color data on the female specimens of *rubribarbus*.

Taxonomy. This species was erroneously considered a subspecies of *homolechis* by Barbour. *Rubribarbus* is actually closely related to *allogus*, and museum specimens are difficult to distinguish from *allogus*: the undivided character of the scale anterior to the nares serves to separate most specimens of *rubribarbus* when color is absent. This species is further distinguishable from *allogus* by the smaller ear opening. However, there is considerable overlap in the latter character and it is therefore not very useful in practice. Some color characters, however, assist in identifying preserved specimens, e.g., the presence of darkly pigmented scales at the base of the dewlap of *rubribarbus*. This usually appears as a dark area in the throat of specimens. In *allogus* usually no dark pigment is visible in the throat. In those specimens of *allogus* that demonstrate a dark throat the pigment is between the scales rather than in the scales as in *rubribarbus*. Some specimens of *rubribarbus* also show

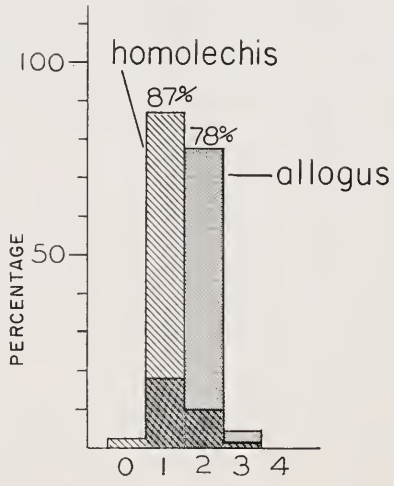

Figure 9. Histograms of the number of scales between the supra-orbital semicircles of *allogus* and *homolechis*. The great majority of the specimens of these two species are distinguishable by this character.

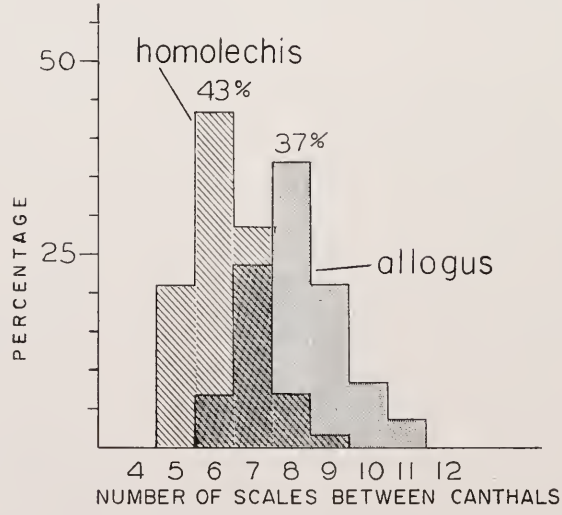

Figure 10. Histograms of the number of scales between the canthals in *homolechis* and *allogus*. There is considerable overlap between the specimens of these two species.

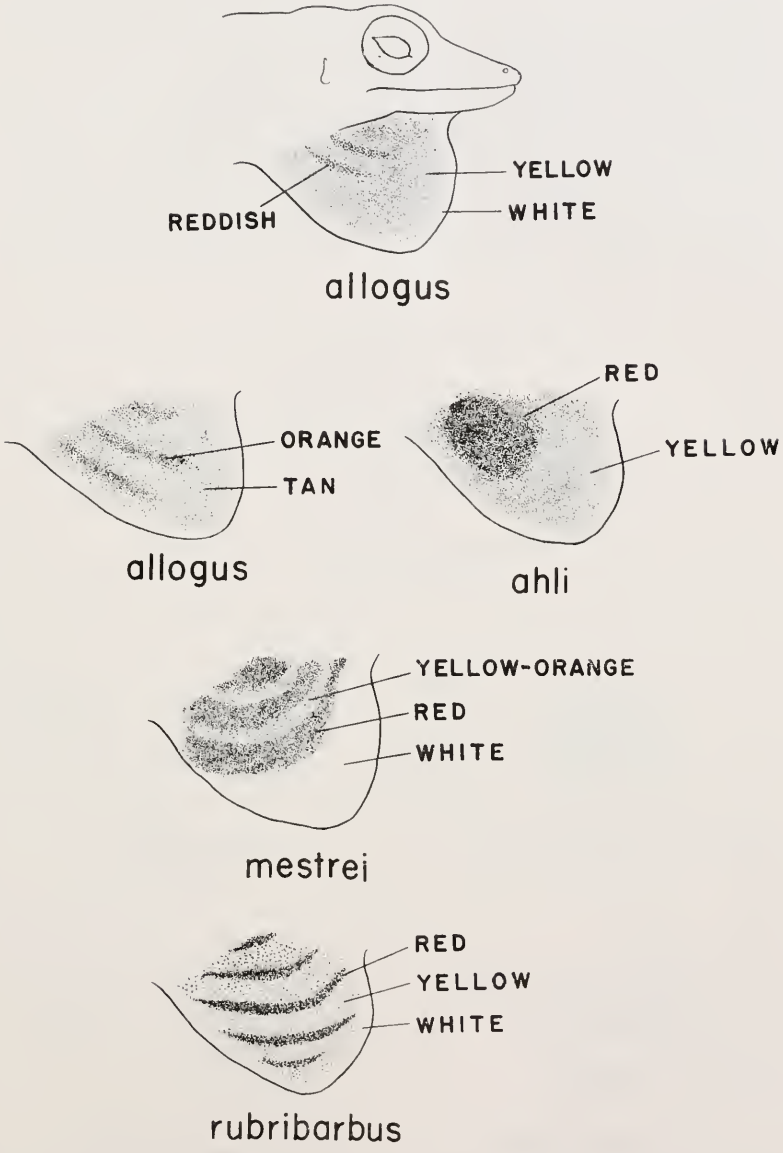

Figure 11. Diagrams of the dewlap pattern and color of *A. allogus*, *ahli*, *rubribarbus*, and *mestrei*.

indications of the dark vertical body stripes which are not present in *allogus*. Also of value in distinguishing *rubribarbus* are the well-marked reticulations on the chin.

In their description (Barbour and Ramsden, 1919), the authors listed M.C.Z. 11941 as the number of the type specimen and gave M.C.Z. 11868 as the number of the paratype (and of the specimen figured in plate 9). There is an evident lapsus since M.C.Z. 11868 is the actual type specimen, while the number 11941 belongs to a specimen of *Platysaurus capensis* from Rhodesia.

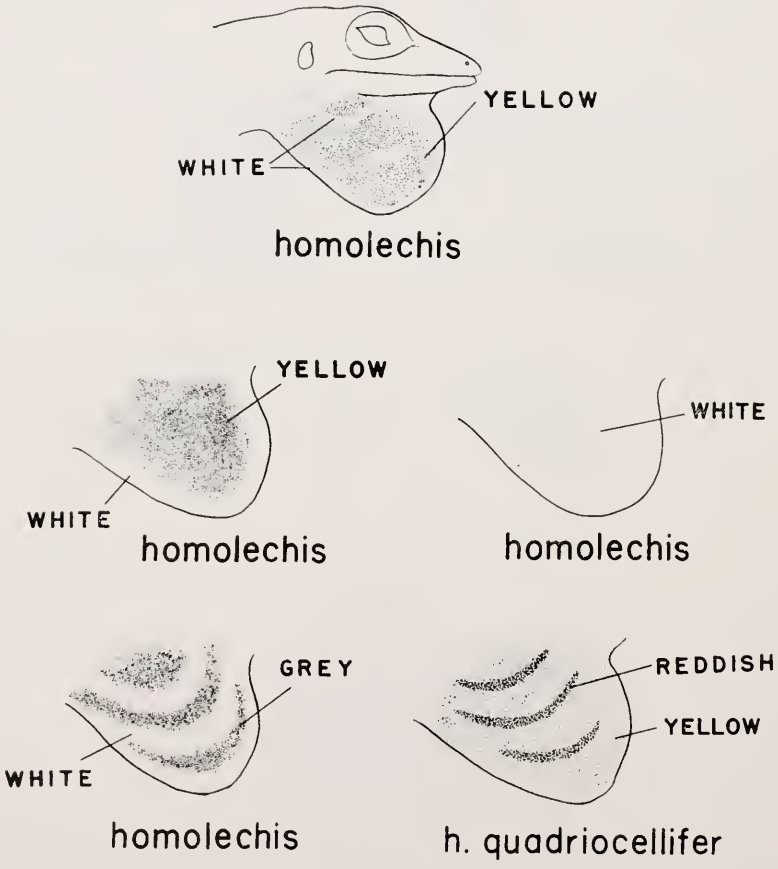

Figure 12. Diagrams of the dewlap pattern and color of *A. homolechis*.

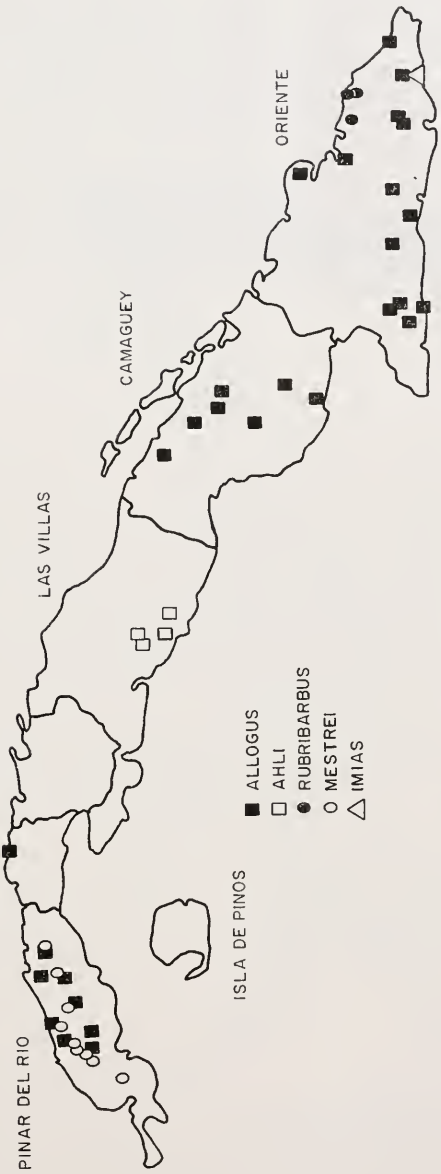

Figure 13. Map of the distribution of *A. allogus, ahli, rubribarbus, mestrei,* and *imias,* sp. nov.

Distribution. This species is allopatric to *allogus*. *Rubribarbus* is so far known only from the northeast coast of Oriente, from Cananova to Punta Gorda to the east of Moa (Figure 13).

Ecology. We have collected this species to the east of Moa in the broad leaf gallery forests that extend along the streams and

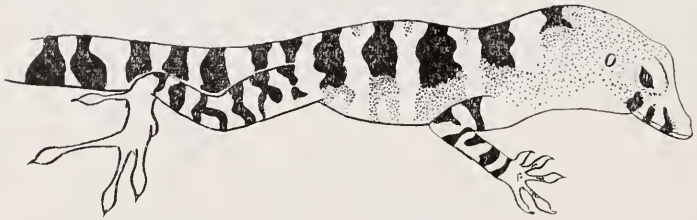

Figure 14. Diagram of the distinctive dark banding of *A. rubribarbus*.

rivers that deseend through the coastal pine forests. We have also collected it in the cooler broad-leaf forests southeast of Moa at an elevation of about 1000 feet. It is a forest-dwelling species but does not appear to be restricted to the deep shaded portions of the forest as are *allogus* and *ahli*. It is a shy species and difficult to observe against the greyish bark of some of the trees. It perches head down a few feet from the ground in the same fashion as the other species.

It is very probable that this species may no longer exist in the vicinity of Cananova, the type locality. We visited this locality briefly in 1959 and were unable to find forests to collect in.

Anolis homolechis (Cope)

Xiphosurus homolechis Cope, 1864.
Anolis homolechis, Boulenger, 1885; Barbour, 1914; Barbour and Ramsden, 1919.
A. calliurus Ahl, 1924.
A. muelleri Ahl, 1924.
A. cubanus Ahl, 1925.
A. patricius Barbour, 1929.
A. homolechis homolechis Barbour, 1937.
A. homolechis patricius Barbour, 1937.
A. quadriocellifer Barbour and Ramsden, 1919.

Type locality: "West Indies." It would be reasonable to restrict the type locality to Habana, Habana Province, Cuba. The

populations in the vicinity of the city of Habana have a pure white dewlap.

Definition. Supraorbital semicircles separated by a single scale (Figures 3 and 9); posterior medial margins of the mentals separated by small postmentals (Figure 6a); supracarpal and supradigital scales usually smooth or with a single keel (Figure 7a); usually 5-7 scales between the first canthals (Figures 3 and 10); a single undivided scale anterior to the nares and in contact with the rostral (Figure 8); scales along the posterior margin of the interparietal large and sharply demarcated from the

Figure 15. Dorsal pattern of the female specimens of *A. homolechis.* In life the pattern is composed of black and various shades of brown.

dorsals (Figure 3). The body/femoral ratio averages 3.6; the head/ear ratio averages 7.7 (Tables 1 and 2). The maximum snout-to-vent length: ♂, 56 mm., ♀, 43 mm.

The general body color ranges from a very light tan, through brown, to black. Usually there is some evidence of horizontal stripes on the lateral surface of the body, and of four dark chevrons on the dorsum. Yellow markings may be present laterally. The iris is gold or metallic brown in color. The dewlap color of this species is very variable (Figure 12) and is discussed below in detail.

The female color pattern usually consists of a series of light colored diamonds on the dorsum (Figure 15). The general color may change from tan to black. The ventral surface is sometimes yellow in females.

Taxonomy. We have examined the types of the three species described by Ahl (*calliurus, muelleri,* and *cubanus*) and consider them synonymous with *homolechis.* We have also examined the type of *A. patricius* Barbour from Mina Piloto in Oriente and find no character to distinguish this form from *homolechis.* The type locality of *patricius* is in the municipality of Sagua de Tanamo but we have been unable to locate Mina Piloto precisely. No information about the dewlap color was provided in the description of the type. The *homolechis* from the town of Sagua de Tanamo and nearby Cananova have a white dewlap.

In the 1937 checklist, Barbour included *A. quadriocellifer* from the Ensenada de Cajon, Cabo San Antonio, at the extreme western end of Cuba, as a subspecies of *homolechis.* We have examined the types as well as additional specimens from the type locality collected by Albert Schwartz. This form is readily distinguishable from the other populations of *homolechis* by the light-margined, dark ocellus above the foreleg (Figure 16), and

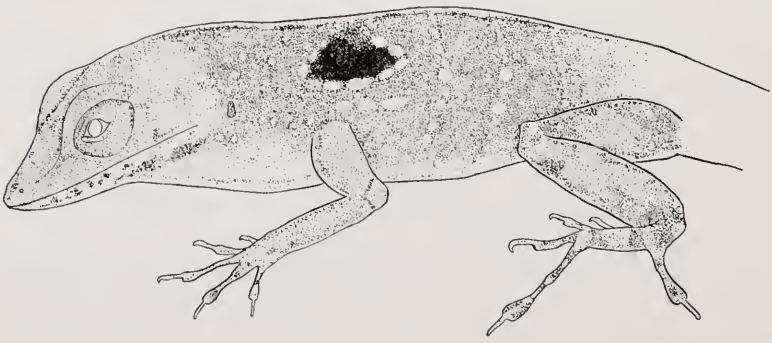

Figure 16. The lateral pattern of a male specimen of *A. homolechis quadriocellifer* (M.C.Z. 11907) from Ensenada de Cajon, Pinar del Rio.

the yellow dewlap with three reddish stripes (Figure 12). The juvenile as well as female specimens of *quadriocellifer* have a well-marked lateral ocellus. We agree with Barbour in considering this form a subspecies of *homolechis*. We have reached this decision from a consideration of the morphology of the populations near the Ensenada de Corrientes as represented by specimens collected by Albert Schwartz and his staff. (The localities are shown on map of Figure 17.)

The Ensenada de Corrientes is midway between Cabo San Antonio, the type area for *quadriocellifer,* and the towns of Cayuco and Isabel Rubio (formerly Mendoza) in the vicinity of which typical white dewlap *homolechis* has been collected.

Specimens from Ensenada de Corrientes have a yellow dewlap and have white spots on the sides of the body that resemble the light-colored margins of the *quadriocellifer* ocelli. Specimens of *quadriocellifer* have most of the supracarpal scales with two or three keels. Specimens from the Ensenada de Corrientes have most of these scales with only one or two keels, and two of the specimens (of a total of 23 males examined) have all the supracarpal scales smooth. Specimens from the vicinity of Cayuco and Isabel Rubio have the supracarpal scales with only a single keel or smooth.

On the basis of these characters we infer that typical *quadriocellifer* from Cabo San Antonio is connected to "typical" *homolechis* from southern Pinar del Rio by an intermediate population (only adult males used in the comparison) as shown in the following table:

quadriocellifer (8 specimens)	Populations from Ensenada de Corrientes (23 specimens)	*homolechis* (14 specimens from SW of Cayuco)
a) Yellow dewlap with red stripes.	a) Yellow dewlap.	a) White dewlap.
b) White-margined lateral ocellus.	b) Lateral white spots.	b) No white spots.
c) Supracarpals usually with 2-3 keels.	c) Supracarpals usually with 1-2 keels.	c) Supracarpals usually with 0-1 keel.

Four of the specimens (representing the three localities listed in the above chart) were unique for *homolechis* in having the ventrals with slight keels.

Variation. No geographical variation was found in the scalation of this species. However, there is a pronounced variation in the color and pattern of the dewlap. The majority of the populations of *homolechis* throughout the island and the Isla de Pinos have a white dewlap. The dewlap may be pure white showing only a faint indication of black pigment or there may be two or three grey stripes on a white background (Figure 12). Both these types show no systematic geographical distribution and may actually be found in the same population. The populations showing these two white patterns may best be referred to as the "white dewlap" form. Another group of variations may be called the "yellow dewlap" form. We have personally seen this form from the Sierra de Cubitas, the shores of the Bahia de Nuevitas, and along the north coast at the Playa Santa Lucia (east of the Bahia de Nuevitas) all in the Province of Camaguey. The Sierra de Cubitas population has a yellow dewlap with a broad white margin (Figure 12). The populations from the vicinity of the Bahia de Nuevitas and Playa Santa Lucia have a deeper yellow or orange color, a narrow white margin, and one or two stripes of white or light yellow (Figure 12). The two yellow dewlap populations are therefore distinguishable. We do not know if these two populations are isolated from each other or not. However, it appears probable that they are separated by the savanna that extends north to the coast near the Rio Maximo.

P. J. Darlington has also recorded yellow (and/or orange) dewlap *homolechis* from the south coast of Oriente near Pico Turquino, Cabo Maisi, and the lower Rio Ovando. Albert Schwartz has also collected the yellow dewlap form along the south coast of Oriente from just north of Cabo Cruz to Playa Juragua, east of Siboney. Yellow dewlap forms have also been recorded at Banes on the north shore of Oriente, and of course the previously mentioned population from the Ensenada de Corrientes in Pinar del Rio has a yellow dewlap. We cannot compare the color patterns of these populations with those of the Camaguey yellow dewlap populations because we have not seen the former in life, and beyond the fact that they are yellow we do not know the details of the pattern.

The map (Figure 17) indicates the known distribution of the white and yellow dewlapped forms. There is an apparent gap in the distribution of the coastal yellow dewlap in southern Oriente between Cabo Maisi and Playa Juragua. In this zone

Figure 17. Map of the distribution of the various forms of *A. homolechis*.

white dewlapped forms have been collected. Similarly, there is an apparent gap on the north coast of Oriente. As mentioned above there is also a gap between the yellow forms of the Sierra de Cubitas and the yellow forms of Playa Santa Lucia in Camaguey. For the moment we believe it prudent to refrain from designating these populations as subspecies or species. With the exception of the Sierra de Cubitas population all of the other yellow forms are coastal. The coastal forests are usually drier and warmer than the more inland forest and the yellow forms may represent a *homolechis* ecotype adapted to the more stringent conditions of the coastal areas. Collecting in the coastal forest in other parts of the island may prove that the yellow form is more widespread than the present data indicate.

We have studied the contact of the yellow and white forms near the Playa Santa Lucia, Camaguey. The senior author undertook field work in this area in 1957 (Ruibal, 1958) and both of us visited the area in 1959. A road runs inland from the beach at Sta. Lucia in a southwesterly direction. Collections were made at various stations along this road from the beach to 21 kilometers inland. At the shore the vegetation is a coastal thicket predominantly made up of seagrape (*Coccoloba*) and a small palm (*Coccothrinax* sp.). A few kilometers inland, broadleaf forest is found on limestone. Some of the forest is in relatively good condition, having only been "highgraded;" other parts have been severely cut for charcoal. Some tongues of mangrove extend into the forest. At about 20 kilometers inland there is only a sparse open forest with very few large trees. Cattle are grazed in the area and most of the vegetation here is "mije" (*Eugenia*), an arborescent cactus (*Dendrocereus*), and numerous species of palms. A total of four visits were made to Santa Lucia to sample the populations. From the thicket on the shore to 12 km. inland only yellow *homolechis* were collected. From 13 km. to 17 km. inland, about 25 specimens of the white dewlap form have been collected, yet within this same area (at the 15 km. and 17 km. stations) two specimens of the yellow form have also been found. From the 18 km. to 21 km. stations only white forms were found. This transition of yellow forms on the coast and white forms further inland is similar to the situation that P. J. Darlington found along the south coast of Oriente where he collected both forms of *homolechis*, the yellow near the coast

and the white inland. No "intermediate" specimens between the two forms have been found in the Sta. Lucia area.[2] The amount of field work done at Sta. Lucia was limited and we did not obtain any ecological or behavioral data on the two forms. As mentioned above, the yellow and white forms of *homolechis* are best left, for the time being, without any taxonomic designation. It is to be hoped that in the near future a more precise study can be made of this interesting problem.

Ecology. Some aspects of the ecology of this species are discussed in Ruibal (1961). In the province of Camaguey this species is restricted to the margins of the broadleaf forests. It is customarily found in areas of filtered sunlight — along paths, small clearings, and the edges of the forests. However, it is found throughout the drier and sparser coastal broadleaf forest where *allogus* is absent. It is also found in the palm-pine savannas in northern Oriente. In Camaguey this species is never found near human habitations or in agricultural areas. In contrast, at Sagua de Tanamo in Oriente, *homolechis* is an abundant lizard of the fence posts around houses and pastures. It occupies the same fence posts with *A. sagrei* and *A. porcatus*. Similarly, near Habana we have observed *homolechis* in gardens. In Las Villas we have had little experience with the species but we always found it in forests or in the vicinity of forests. It is interesting that the restriction of *homolechis* to forest habitats in central Cuba may be correlated with the presence of *A. allisoni* (Ruibal and Williams, 1961) around human habitations in central Cuba. It may be that in eastern and western Cuba *homolechis* can occupy the area around human habitations because *allisoni* is absent (in these areas *porcatus* replaces *allisoni* [see Ruibal and Williams, *op. cit.*]).

Male specimens of *homolechis* are characteristically found perched head down on small tree trunks a few feet off the ground. The tail is often curled laterally. The females are more terrestrial and are usually on the ground or on perches closer to the ground than the males.

This species is found throughout the forests of the Sierra Maestra and has been collected as high as 5900 feet at Palma Mocha, near Pico Turquino.

[2] One specimen collected at 12 km. from the beach in 1957 had a red ground color to the dewlap and yellow stripes.

Anolis mestrei Barbour and Ramsden

A. mestrei Barbour and Ramsden, 1916.
A. allogus mestrei, Barbour, 1937.

Type locality. Valle de Luis Lazo, Pinar del Rio, Cuba.

Definition. Except for one character, we have been unable to successfully distinguish the scalation of this species from that of *homolechis*: Specimens of *mestrei* have small granular posterior supraciliaries while most *homolechis* have larger, elongate, and keeled posterior supraciliaries. This character is variable, however, often subjective, and difficult to use. *Mestrei* further differs from *homolechis* in having longer hind legs, the body/femoral ratio averaging 3.2 (Table 1) and a smaller ear opening, the head/ear ratio averaging 8.5 (Table 2). The maximum snout-to-vent length ♂, 55 mm., ♀, 44 mm.

The body color of this species varies from dark to light grey with an overall greenish cast. Yellow or orange spots are present over the body. The iris is yellowish. The dewlap has a dark red basal spot with two yellow-orange stripes. The remaining broad margin is white (Figure 11). The scales on the dewlap are white.

The females show the same general body color but can also shift to a light brown color. There are darker hour-glass shaped markings on the dorsum. The females have a small apricot colored dewlap.

Taxonomy. An examination of the type and paratypes has revealed that two species were confused in the original description. The type (M.C.Z. 11285) and paratypes (M.C.Z. 11286, U.S.N.M. 26731 and 26733) are *mestrei* while two other paratypes (U.S.N.M. 26732 and 26344) are actually specimens of *allogus*.

Barbour was in error in making *mestrei* a subspecies of *allogus* in the 1937 checklist. *Mestrei* is readily distinguishable from *allogus* by many scale and color differences. In the limestone hills of Pinar del Rio the two species are sympatric.

Preserved specimens of *mestrei* are very difficult to distinguish from *homolechis*. Usually there is a dark basal portion to the dewlap in preserved specimens of *mestrei*. The supereiliaries, the length of the hind limbs, and the smaller ear opening will also assist in distinguishing specimens. The ear opening in *mestrei* is not only smaller (in height) but is also differently shaped than in *homolechis*. In *mestrei* the opening is circular while in *homolechis* it is higher than wide. This is readily apparent in

the comparison of the ear height/ear width ratio of the two species:

	homolechis (15 specimens)	*mestrei* (15 specimens)
Mean	1.59	1.03
Range	1.2-2.1	0.9-1.4

Distribution. This species is restricted to the broadleaf forests of the limestone mountains and hills of Pinar del Rio — the Sierra de los Organos and the Sierra del Rosario.

Ecology. We have observed this species in a forest in a small "mogote" near Sumidero. Here *mestrei* was found throughout the forested portion of the mogote. The females and juveniles were on the ground or on the boulders of limestone that covered much of the forest floor. The adult males appear to be restricted to the limestone or were found on fallen logs near the limestone outcrops. In no instance did we find the *mestrei* perched head down on vertical tree trunks in the manner of *allogus* and *homolechis*. The lizards would escape by running to the ground and hiding, or by entering crevasses in the limestone. We started collecting at this locality at 8:00 in the morning and during the early part of the morning only juveniles and females were seen, and it was not until near noon that we observed the adult males. This species appears to be restricted to the shaded portions of the forest and only in a few instances was it found in areas of filtered sunlight.

Anolis imias, sp. nov.

Type: M.C.Z. 42556, adult male, collected east of Guantanamo Bay at Imias, on the south coast of Oriente Province, Cuba, in August 1936, by P. J. Darlington.

Paratype. M.C.Z. 42555, adult female having the same data as the type.

Diagnosis. Similar to *A. homolechis* but differing from that species in having smooth brachial scales, smooth supraoculars, larger ear opening, longer hind limbs, the gulars bordering the mental along a transverse suture, and a brown dewlap.

Description of type. Head. Most of the head scales smooth, the anterior-most scales with blunt keels. Six scales across the snout between the first canthals. A frontal depression and weakly developed frontal ridges. Nostril separated from the

rostral by two scales on the right side and by one scale on the left side. Seven scales bordering the rostral posteriorly. Supraorbital semicircles separated from each other by a single row of small scales. Supraoculars irregular in shape, smooth, and separated from the supraorbitals by a row of scales. Canthus well-marked. Four rows of loreals below the second canthal. Suboculars keeled and in contact with the supralabials. The subocular ring is continuous with a group of slightly enlarged postoculars. Eight supralabials. A large interparietal with no evidence of a parietal eye. Parietal region in a depression demarcated posteriorly by the V-shaped ridge of the underlying parietal bone. Postparietal scales large and sharply demarcated from dorsals. Temporals small, the upper temporals forming a longitudinal zone of scales larger than the granular lower temporals and larger than the scales between the upper temporals and the parietals. Ear opening vertically elongate.

Mental longitudinally divided, bordered along a straight transverse contact by four small gulars. The mental is also bordered posteriorly by a pair of sublabials and infralabials. Throat and chin scales smooth. Dewlap large and with smooth scales.

Body. Middorsal scales keeled and larger than the lateral granular scales, but not sharply demarcated. Ventrals smooth, imbricate, with a convex posterior margin, and in longitudinal and diagonal rows.

Limbs. Humeral scales with weak keels, but the larger brachial scales are smooth. Hind limb scales smooth with the exception of the small scales on the dorsal surface of the limbs. Most scales of the pes and manus smooth; if keeled only with a single weak keel.

Tail. Laterally compressed, with a high crest, and with all the scales keeled. Verticils not readily distinguishable.

Measurements. Snout-to-vent, 65 mm.; head, 18 mm.; femoral length, 21 mm.; ear height, 3 mm. Body/femoral ratio = 3.1, and the head/ear ratio = 6.0.

Description of the paratype. The female paratype resembles the type in all respects except the following: all the head scales keeled; both nostrils separated from the rostral by a single scale; supraorbital semicircles separated by a double row of small scales; rostral bordered posteriorly by six scales; mental bordered posteriorly by only two small gulars along a straight margin; tail slightly compressed but without a crest.

Measurements. Snout-to-vent, 46 mm.; head, 13 mm.; femur, 14 mm.; height of ear, 2 mm.

Color. According to the collector, P. J. Darlington, the type had a brown dewlap in life. As preserved, the only distinctive markings are 12 vertical dark bands on the tail that are separated from each other by narrower lighter bands. Each hind limb has six transverse dark bands, and the forelimb shows evidence of about four transverse dark bands. The dorsum (from the nape to the base of the tail) shows five indistinct, dark crossbands. The chin has reticular markings.

The female paratype has the chin covered with dark reticulations that are continuous with the dark vertical marks on the labials. The body shows no discernible pattern.

Remarks. Though morphologically similar to *homolechis* the new species is a very distinctive form. The smooth head scales and brachials set it off from all the other members of the *homolechis* group. It resembles *allogus* in the postmental-mental suture, the long hind limbs, and large ear opening.

P. J. Darlington also collected *homolechis* at Imias, but did not collect any *allogus*. It is therefore possible that *imias* may be the ecological equivalent of *allogus*.

DISCUSSION

Ecology. We have observed *homolechis* and *allogus* in broadleaf forest localities in Pinar del Rio, Camaguey and Oriente. At all of these localities both species proved to have identical perching habits (head down, a few feet from the ground, on tree trunks) but were ecologically separated, *allogus* being restricted to the deeper shaded portions of the forest while *homolechis* was found in the small clearings and paths or in the sparser portions of the forest. In the forest habitat *homolechis* dwells in the filtered sunlight areas rather than in the deep shade (where *allogus* is found) or in the open full sun areas (where *sagrei* is found). This distinction between the species is reflected in the mean body temperature of the species — *homolechis* having a mean body temperature of 31.8°C. in contrast to 29.2°C for *allogus* (Ruibal, 1961).

Our experience with *ahli* in the Sierra de Trinidad leads us to believe that *ahli* resembles *allogus* in its ecology. In the Sierra de Trinidad we succeeded in finding *ahli* only in the deeply

shaded portions of the forest. Our limited experience with *rubribarbus* in the vicinity of Moa indicated that this species may not be as restricted to shade as *allogus*. Most of the specimens of *rubribarbus* were collected in a portion of the hardwood gallery forest that had been partially burned. The specimens of *rubribarbus* were seen on the exposed tree trunks in the clearings.

A. mestrei is apparently a shade-dwelling form like *allogus*. However, it is distinguished from the other species in apparently being restricted to limestone substratum, rather than to tree trunks.

A. homolechis is characterized by a wider tolerance of habitats than the other species mentioned above. It is not restricted to the forests, and in eastern and western Cuba is found associated with *sagrei* in the vicinity of human dwellings.

Distribution. Both maps (Figures 13 and 17) demonstrate distributional gaps of *homolechis* and *allogus* in the region of Matanzas and most of Las Villas. A similar gap occurs in N.W. Oriente where no records of either species are known. We believe that these are apparent gaps and that they are the consequence of two factors:

1. Matanzas and Las Villas are intensively cultivated and the natural forest habitat of these species has been almost completely obliterated. *Allogus* is nowhere known to survive outside of its shade-forest habitat and *homolechis* is only sometimes found outside of the forest. Before the advent of agriculture most of the vegetation of these provinces was hardwood forest and it can be assumed that these two species were then common and widespread in these areas.

2. These areas are poorly collected and if appropriate habitats still exist they have not been visited by herpetological collectors.

It is of interest that similar distributional gaps exist for *A. porcatus* and *A. allisoni* (Ruibal and Williams, 1961).

One question that further collecting in Las Villas may answer is the relation of *ahli* to *allogus*. Our data so far indicate that *ahli* is restricted to the Sierra de Trinidad; however, we have no information whatever about the portions of Las Villas outside of these mountains.

We lack similar information in respect to the zone of contact between *allogus* and *rubribarbus*. If intermediates between these two forms are found along the northern coast of Oriente it would be necessary to reduce *rubribarbus* and *allogus* to subspecies.

The distribution of the various species of this group can be summarized in the following manner:

1. Islandwide distribution. The species sympatric, but ecologically isolated from each other:

homolechis and *allogus*

2. Local species inhabiting restricted areas and occupying an ecological niche comparable to that of *allogus*. These species are all allopatric to *allogus*:

ahli, rubribarbus (?), and *imias* (?)

3. Local species inhabiting restricted areas and occupying an ecological niche comparable to that of *allogus*, differing, however, in the substratum selected for perching. Sympatric with *allogus*:

mestrei

Relationships. The six species of the *homolechis* group are closely related, and as has been mentioned previously some of the forms cannot be adequately distinguished by scale characters. The two most distinctive forms are *allogus* and *homolechis*. The six species can be grouped in the following manner:

allogus *ahli* *rubribarbus*	Very similar, not readily distinguishable except by color.
homolechis *mestrei*	Very similar, not readily distinguishable except by color.
imias	Appears to be closer to *homolechis* than to *allogus*.

Another species which is closely related to these species, and may actually merit being included in the group is *A. sagrei*. So far the only distinguishing character of squamation that we have been able to find to separate *sagrei* from the *homolechis* group (especially *homolechis* itself) is the keeled mucronate condition of the ventral scales in *sagrei*, and this keeling may sometimes be very weak and even apparently absent (e.g. in some specimens from Trinidad, Las Villas). *Sagrei* does, of course, differ from *homolechis* and all other members of the *homelechis* group in dewlap color and in thermal requirements and ecology.

In Table 3 the various characters used in distinguishing species of the *homolechis* group are tabulated to facilitate a comparison of the six forms.

TABLE 3. THE CHARACTERS USED IN DISTINGUISHING THE SPECIES

Characters	*allogus*	*ahli*	*rubribarbus*	*homolechis*	*mestrei*	*imias*
Number of scales separating supraorbital semicircles	2	2	2	1	1	1-2(?)
Posterior medial margins of mentals separated by small postmentals	No	No	No	Yes	Yes	No
Supradigitals and supracarpals multicarinate and mucronate	Yes	Yes	Yes	No	No	No
Number of scales between the first canthals	7-9	7-9	7-9	5-7	5-7	6

	allogus	*ahli*	*rubribarbus*	*homolechis*	*mestrei*	*imias*
Scale anterior to naris divided or single	Divided	Divided	Single	Single	Single	Single
Scales around interparietal large	No	No	No	Yes	Yes	Yes
Average head/ear ratio	6.2	6.3	7.6	7.7	8.5	6.0
Average body/femoral ratio	3.3	3.3	3.3	3.6	3.2	3.1
Iris Color	Blue	Blue	Blue-grey	Yellow	Yellow	?
General body color	Reddish	Brown with greenish cast	Greyish	Brown-black	Grey with greenish cast	?
Dewlap color	Tan or yellowish with 2-4 reddish stripes	Yellowish with a red basal spot	Yellow with 4-5 red stripes and a white border	Variable (See Fig. 12)	Red basal spot with yellow stripes and a broad white margin	Brown

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LIST OF LOCALITIES

A. allogus

PINAR DEL RIO: Sumidero; near Cabezas; 13.5 km. S. of Las Pozas; Rangel; San Vicente; San Diego de los Baños; 8 km. E. of Matahambre; Pinar del Rio; Soroa.

HABANA: 6.8 m. W. of Jaruco.

CAMAGUEY: 15 km. S.W. of Camaguey; nr. Banao, Sierra de Cubitas; S. of Jaronu; Sierra de Najasa; 7 km. S.E. of Sta. Cruz del Sur; Loma de Cunagua.

ORIENTE: Mal Paso, nr. Guantanamo; Monte Libano, nr. Guantanamo; Bueycito; Los Negros, nr. Jiguani; Baracoa; coast S. of Pico Turquino; Cobre Range, Sierra Maestra; Palma Mocha Mts., Sierra Maestra; Banes; Pico Turquino; nr. Buey Arriba; 16 m. E. of Mayari; Jutinicu; mts. N. of Imias.

A. ahli

LAS VILLAS: Electric plant, Sierra de Trinidad; nr. Camanayagua, Sierra de Trinidad; W. slope of Sierra de Trinidad; S. of Topes de Collantes; Habanilla Falls, Sierra de Trinidad; 4 km. W., 12 km. N. of Trinidad.

A. rubribarbus

ORIENTE: nr. Moa; Cananova; Mina Piloto.

A. mestrei

PINAR DEL RIO: San Vicente; 10 km. W. of Cabezas; 10 km. N. of Cabezas; 2.9 km. E. of Isabel Rubio; Soroa; 8 km. E. of Matahambre; Rangel; San Diego de los Baños; Luis Lazo; Sumidero.

A. imias

ORIENTE: Imias.

Anolis homolechis homolechis

(Localities preceded by an asterisk denote yellow dewlap populations)

PINAR DEL RIO: Luis Lazo; Guane; Sumidero; nr. Consolacion del Sur; San Diego de los Baños; San Vicente; N. of San Vicente; nr. Cabezas; Soroa; 7.6 ml. E. Isabel Rubio; 2.9 ml. E. Isabel Rubio; 7-10 km. S.W. of Cayuco; *N. shore Ensenada de Corrientes; *W. coast Cabo Corrientes; 8.5 ml. E. Cabañas; San Cristobal; 1 m. N. of La Coloma; nr. Viñales.

HABANA: 9 km. S.W. San Jose de las Lajas; Playa de Guanabo, E. of Habana; Jibacoa; Isla de Pinos (various localities); Habana, nr. Rancho Boyero; Habana; San Antonio de los Baños; Madruga.

MATANZAS: Pan de Matanzas; 6 km. N.E. of Matanzas; 5 km. N.E. of Canasi.

LAS VILLAS: Topes de Collantes, Sierra de Trinidad; Central Soledad; Sierra de Jatibonico.

CAMAGUEY: 15 km. S.W. of Camaguey; Sierra de Najasa; 27 km. W. of Ciego de Avila; about 15 km. S.W. of Vertientes; 7-8 km. N.E. of Santa Cruz del Sur; *Sierra de Cubitas; *nr. Banao; *Bahia de Nuevitas, San Jacinto; *Bahia de Nuevitas, Los Ballenatos; *Loma de Cunagua, 12 m. E. of Moron; *between Esmeralda and Jaronu; *S. of Jaronu; 0.6 ml. N. of Majagua; Marti: Cuatro Caminos; *Playa Sta. Lucia and a number of localities S.W. of Sta. Lucia.

ORIENTE: Guantanamo; Sagua de Tanamo; Cananova; nr. Moa; 16 km. E. of Mayari; nr. Buey Arriba; Birama; Pico Turquino; *Coast S. of Pico Turquino; Mina Piloto; Buenos Aires; near Santiago; *Banes; *Cabo Maisi; Los Negros, nr. Jiguani; Baracoa; *lower Rio Ovando; Sierra del Cobre; *Cabo Cruz; N. of Imias; Imias; *Playa Juragua, nr. Siboney; *between Belic and Cabo Cruz.

A. homolechis quadriocellifer

PINAR DEL RIO: Ensenada de Cajon; Cabo San Antonio.

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TAXONOMY OF THE DEEP SEA FISHES OF THE GENUS *CHAULIODUS*

By James E. Morrow, Jr.
Department of Wildlife Management
University of Alaska, College, Alaska

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
October, 1961

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No. 9 — Taxonomy of the Deep Sea Fishes of the Genus Chauliodus

By James E. Morrow, Jr.[1]

Representatives of the genus *Chauliodus* are found in all the oceans of the world in temperate and tropical regions, and form a rather closely knit group. Some species are widespread in their distribution; others appear to be confined to particular water masses. Among the more widely ranging forms, populations appear to differ from one water mass to another, with the result that a number of species and subspecies have been described.

The various forms of *Chauliodus* are not particularly well defined in much of the literature, nor are they always easy to distinguish when specimens are at hand. The older descriptions, in particular, made no allowance for normal variation within species, and are, almost without exception, so brief and generalized that it is well nigh impossible to determine what form was being described. Yet the authors of the past cannot really be blamed for this. Specimens were even more difficult to obtain in those days than they are now, and taxonomic thought of the time was a far cry from modern ideas.

In 1906, Brauer gave a summary, based on the literature, of the species then known, but it was not until the expeditions of the Dana that a series of specimens adequate for modern taxonomic techniques became available. Basing their account on the specimens collected in the Atlantic by the Dana expedition of 1920-22, Regan and Trewavas (1929) produced the first modern work on *Chauliodus*. They described a new species, *C. danae*, distinguishing it from *C. sloani* chiefly on the basis of the more posterior position of the dorsal fin and a different structure of the chin barbel.

Later, Ege (1948) studied the large collections of *Chauliodus* from the round-the-world Dana cruise of 1928-30. He described two new subspecies of *C. sloani* (*C. s. secundus* from the Indo-Pacific and *C. s. schmidti* from the eastern Atlantic) and reduced several other species to the status of subspecies of *C. sloani*. Haffner (1952b), studying the zoogeography of the genus, accepted Ege's classification, though with some reservations as to the propriety of the subspecific designations of some groups. Since that time, virtually nothing has been done with the group as far

[1] Former address: Bingham Oceanographic Laboratory, Yale University.

as published information is concerned, although exploratory fishing, particularly in the north and central Pacific, has added a great deal to our knowledge of the range of several species.

ACKNOWLEDGEMENTS

In carrying out the present work, we have had available to us the large collections from the Dana Expedition 1928-30: the Museum of Comparative Zoology, Harvard University; the United States National Museum; the Department of Oceanography, University of Washington;[1] and the Bingham Oceanographic Collection, Yale University. In addition, we have been able to examine other specimens from the British Museum (Natural History); the Galathea Expeditions 1950-1952; the Marine Laboratory, University of Miami; the Scripps Institution of Oceanography; the Zoological Museum, Stanford University; the Department of Fisheries, University of Washington; and the U.S. Fish and Wildlife Service Laboratory, Honolulu. This material has been made available through the kind cooperation of the following, to whom gratitude and thanks are tendered: Dr. William Aron, Dr. E. Bertelsen, Dr. Henry B. Bigelow, Dr. Anton Bruun, Mrs. M. Dick, Dr. Alfred Ebeling, Dr. Robert Kanazawa, Dr. Ernest Lachner, Dr. Jørgen Nielsen, Dr. C. R. Robins, Mr. R. Rosenblatt, Dr. W. F. Royce, Dr. F. G. W. Smith, Dr. Leonard P. Schultz, Miss M. Storey, Dr. Ralph Taylor, and Dr. Ethelwyn Trewavas.

DIAGNOSTIC CRITERIA

Early descriptions of species of *Chauliodus* depended in the main upon the customary fin ray counts and body proportions.

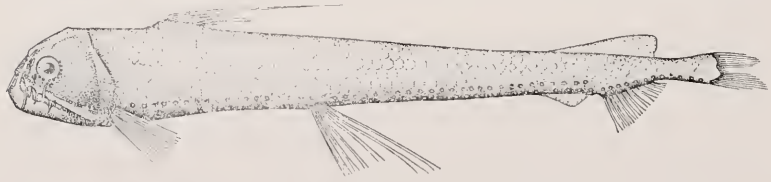

Figure 1. *Chauliodus sloani*. Drawn from several specimens in the Bingham Oceanographic Collection by Shirley P. Hartman.

[1] The material from the University of Washington, Department of Oceanography was collected by Dr. Wm. Aron. His work was supported by the National Science Foundation and by the Office of Naval Research, Contract 477 (10).

Garman (1899) appears to have been the first to realize that the number of serial photophores could be of some taxonomic importance in the group, in which he was followed by Brauer (1906). Ege (1934), studying the related genus *Stomias,* discovered there that the number and arrangement of the small body photophores were characteristic for the various species. In his subsequent work on *Chauliodus* (Ege, 1948), he continued with this same line of thought, placing rather heavy emphasis on the number and type of organ in each scale area, as well as utilizing other characters such as the relative size of certain small body photophores, number and size of teeth, number of lower jaw denticles, etc. However, Ege appears to have based his conclusions with respect to these more minute characteristics upon the examination of a rather small number of specimens. Thus, in dealing with the number and size of the small light organs in the various scale areas, he describes only one or two specimens for each form. Similarly, with respect to teeth and lower jaw denticles, he tabulates data for only four or five specimens of each species. It seemed necessary, therefore, to subject these and other matters to a statistical examination, based on as many specimens as possible.

We therefore turn now to an examination of the various criteria which have been used for the diagnosis of the several species of *Chauliodus.* For this examination, we have used as many specimens as possible of each species. With respect to the serial photophores, we have made use, wherever possible, of the data of other authors as well as our own. It will be noted that there are discrepancies here and there between the number of specimens listed as study material and the number actually used in certain computations. This is due to the delicate nature of these fishes, with the result that they are easily damaged in capture and preservation, so that the character in question could not be observed with the desired degree of accuracy.

Pre-anal distance less head length is measured from the tip of the snout to the base of the first ray of the anal fin. The head is measured from the tip of the snout to the posterior edge of the opercular membrane, with the head as nearly as possible in a normal position. Expressed as a percentage of the standard length, this measurement has been used to set off *C. barbatus* from all other species. However, as shown in Figure 2, *barbatus* is completely overlapped in this respect by *macouni,* and to a great extent by *sloani* as well. To a lesser degree, *schmidti* and *pammelas* also fall within range of *barbatus* for

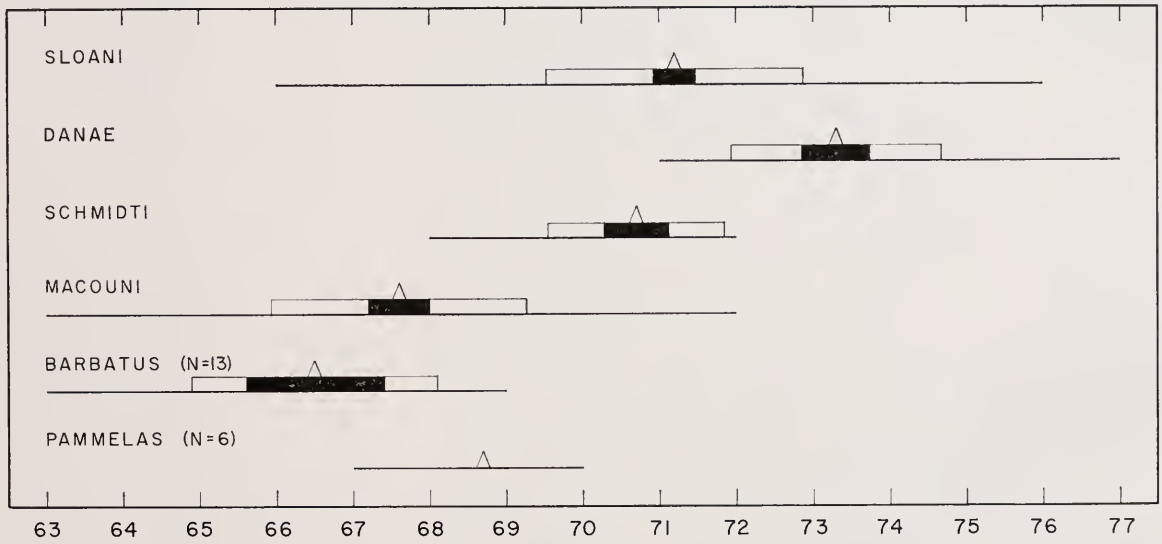

Figure 2. Distribution of pre-anal distance less head length, expressed as percentage of standard length. The range of variation is shown by the heavy base line, with the mean indicated by the point of the inverted V above. One standard deviation and two standard errors on each side of the mean are shown by the white and black bars respectively.

this character. Although some of the differences which appear in Figure 2 are certainly significant, both statistically and biologically, this character is really useful only to separate *barbatus* and *pammelas* from *danae*.

Relative length of third and fourth premaxillary teeth has also been used to separate *barbatus* from the other species. In *C. barbatus*, and also in *C. macouni*, the third premaxillary tooth is always longer than the fourth. In all the other species, the opposite is true. Rarely in *C. sloani* and *C. schmidti* does one find an individual whose premaxillary teeth do not fall into the usual pattern, and the difference in the length of the teeth is usually very slight in such instances. In nearly all the species, there are also occasional individuals whose third and fourth premaxillary teeth are of about equal length, but again, these are rather rare (see Table I). The relative length of the third and fourth premaxillary teeth, then, appears to be a fairly good character for separating the two strictly Pacific Ocean forms from the others.

TABLE I

Relative lengths of the third and fourth premaxillary teeth in *Chauliodus*. The body of the table lists the number of specimens of each species in each category.

Species	3rd tooth longer	4th tooth longer	About equal
sloani	7	101	9
danae	0	36	2
schmidti	2	20	5
pammelas	0	5	0
barbatus	16	0	2
macouni	64	0	2

The number of light organs in each scale area of the second, third and fourth rows has also been considered as diagnostic. In the second row, each scale area generally has two organs in *C. sloani, C. pammelas, C. danae,* and *C. macouni.* In *C. schmidti* and some populations of *C. sloani,* there is a tendency for only a single organ to be present, and in *C. barbatus* it is a rare individual that has more than one much reduced organ present in the second row areas. However, there is a great deal of variation, particularly in *C. sloani,* where we have found 1, 2 or 3 organs in these second row areas. Some indication of this degree of variation is shown in Table II, comparing *C. sloani, C. schmidti* and the *dannevigi* population of *C. sloani.* It is apparent from this

table that the number of small photophores in the second row is not diagnostic for *C. schmidti,* although there is a tendency towards reduction in this form. The same is true for the *dannevigi* population of *C. sloani.* Particularly when it is realized that many Mediterranean specimens match perfectly the descriptions of *dannevigi* with respect to the arrangement of small photophores, there seems no reason to consider *dannevigi* as anything more than a population of *C. sloani.*

TABLE II

Distribution of the number of light organs in the scale areas of the second row in three forms of *Chauliodus.* The body of the table shows the number of specimens of each species with the indicated percentage of second row organs containing two small photophores.

	Percentage of second row areas with two light organs										
Species	0	10	20	30	40	50	60	70	80	90	100
sloani	5	4	4	3	2	8	3	5	5	7	21
schmidti	9	6	1	1	0	3	0	0	1	0	0
dannevigi	2	3	3	1	0	0	5	0	0	1	1

In the scale areas of the third row, there are always two small photophores, except in *C. barbatus.* In that species there are three or more, arranged in a cluster of one slightly larger organ with two to many tiny organs. One specimen of *C. barbatus* examined by us appeared to have but two organs in about half of the third row scale areas, but as the skin of this fish was in very poor condition, this appearance may have been due to damage. The number of organs in the third row, then, will distinguish *C. barbatus* from all other species of the genus.

The scale areas of the fourth row each have two organs, as a general rule, in all species except *C. barbatus* and *C. macouni.* In these, the usual number is one. But in all forms, there is a considerable amount of variation. In *C. barbatus* and *C. macouni,* counts of fourth row organs vary from one to four, in *C. sloani* from one to three. We regard the number of organs in the fourth row scale areas as of only limited value in distinguishing the species of *Chauliodus.*

The number of teeth in the lower jaw has several times been used in the past in attempts to diagnose the species of *Chauliodus,* but it requires only a glance at Table III to see that the number of larger lower jaw teeth is of little taxonomic value. With such a range of variation as is shown here, the best that can be done

is to say that there are differences in the average number of teeth in the lower jaw. *C. sloani* generally has six or seven teeth. *C. danae* most frequently has seven or eight teeth in the lower jaw, but there may be as few as five or as many as eleven. *C. schmidti* most often shows six teeth, *C. barbatus* and *C. macouni* six or seven, and the few specimens of *C. pammelas* that have been examined or reported in the literature all had only five teeth in the lower jaw.

TABLE III

Number of larger lower jaw teeth in various species of *Chauliodus*. The body of the table shows the number of specimens of each species. The data presented here include also tooth counts from Ege (1948).

	Number of Teeth						
Species	5	6	7	8	9	10	11
sloani	9	42	57	13	6		
danae	1	7	23	20	7	2	3
schmidti	5	23	7	3	1		
barbatus	0	7	5	1	1		
macouni	5	46	24	5	1		
pammelas	9						

Also in the lower jaw, the number of small denticles that may occur posteriorly, near the rictus, was used by Ege (1948) to separate *C. schmidti* and *C. pammelas*. Both our own observations and Ege's published data indicate that in *C. pammelas* the number of lower jaw denticles is a function of the size of the specimen. With this limitation in mind, it can be seen from Table IV that the number of lower jaw denticles can be a useful secondary character to distinguish these two species from each other, though it is of relatively little value amongst the others.

TABLE IV

Number of denticles in the lower jaw in *Chauliodus**

Species	0	1	2	3	4	5	6	7	8	9	10 or more
sloani	23	13	11	5	6	8	7	1	0	2	4
danae	27	3	4	9	6	1			**		
schmidti	17	1	1								
barbatus	5	3	5	3	1	1					
macouni	57	6	4	1	1						
pammelas		1				1	1		1		5

* Includes data published by Ege (1948) for 36 *C. sloani*, 7 *C. danae*, 4 *C. barbatus* and 4 *C. pammelas*.

** Regan and Trewavas (1929) give 3 to 8 denticles for *C. danae*.

The relative lengths of the first and second premaxillary teeth have been indicated as a distinguishing feature by which *C. macouni* might be separated from the other forms. The single specimen of *C. macouni* taken by the Dana had a remarkably short first premaxillary tooth, only 51.5 per cent of the length of the second. In all other species, with a few rare individual exceptions, the first premaxillary tooth is 60 per cent or more of the length of the second. This difference does not, unfortunately, hold good. All of the specimens of *C. macouni* examined by us have shown the first premaxillary tooth to be at least 60 per cent of the length of the second. We have found short first teeth only in *C. barbatus*. It may be of interest to note that all our specimens of *C. macouni* came from the northern part of the Pacific, whereas the Dana specimen was found in the tropics, west of the Galapagos Islands. It may be that the short teeth are somehow related to some characteristic of the Pacific Equatorial water mass, where *C. barbatus* also occurs. It may be mentioned here that the Dana specimen of *C. macouni* does not appear to have been mis-identified. Dr. Ege kindly re-examined the specimen, paying particular attention to the postocular photophore. The elongate, pointed shape of this organ and its location well behind the eye leave no doubt that it was correctly named.

Ege (1948: 138, 139) erected a new subspecies of *C. sloani* — *C. sloani secundus* — chiefly on the basis of slightly larger light organs in the scale areas of the first and fifth rows in his new form. He found that in *C. sloani* (*sensu stricto*) the small organs of the first row had a diameter of 4.0 to 4.8 per cent of the average length of the scale areas of the second row. In the same species, the length of the largest organ in the scale areas of the fifth row was 8.9 to 11.0 per cent of the average length of the same scale areas in one group, 11.4 to 11.7 per cent in another group. By contrast, the corresponding values for his new form were given as 6.8 per cent for the dorsal row and 12.5 per cent for the fifth row.

Examining specimens of *C. sloani* from the Atlantic, we observed an extremely wide range of variation in these two characters, leading us to make a detailed study of the matter. The length of the scale areas of the second row was measured on five consecutive scales on each specimen, beginning at the fifth scale behind the base of the ventral fins, and the average taken. The diameter of the appropriate light organ of the corresponding scales of the first and fifth rows was measured and expressed as

a percentage of the average length of the scale areas of the second row. This was done with 64 specimens of *C. sloani* from the Atlantic, 12 specimens of *C. s. secundus* from the Indo-Pacific area, and 13 specimens of *C. sloani* from either the same localities as the *C. s. secundus* or from nearby stations. There was thus a total of 320 photophores from each row measured in the Atlantic sample, and 60 or 65 in each of the others.

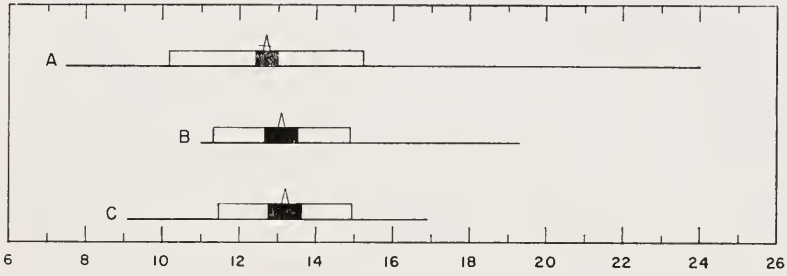

Figure 3. Distribution of the greatest diameter of the large light organ in the fifth row, expressed as percentages of the average diameter of the scale areas of the second row. A) *C. sloani* from the Atlantic. B) *C. sloani* from the Indo-Pacific. C) *C. sloani secundus.*

Figure 3 shows the mean, range, ± two standard errors, and ± one standard deviation for the photophores of the fifth scale row. There is obviously no significant difference in the value of the mean for the three distributions. The distribution of *C. s. secundus* is quite symmetrical, while the two samples of *C. sloani* are skewed to the left. What significance, if any, this may have we are not able to say.

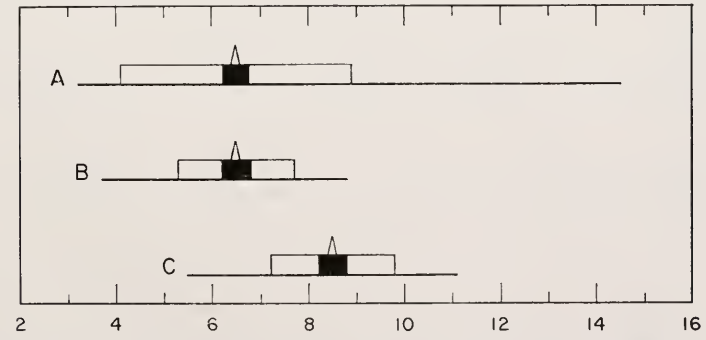

Figure 4. Distribution of the diameter of the light organ in scale areas of the first row, expressed as percentages of the average diameter of the scale areas of the second row. Lettering as in Figure 3.

A similar plot for the photophore of the first row is shown in Figure 4. Here there is an observable difference between the mean value for *C. s. secundus* and the two samples of *C. sloani.* However, the standard deviations of the distributions overlap each other to a considerable degree, indicating a good deal less than subspecific divergence.

The skewness of the Atlantic distribution, in particular, arouses curiosity. The actual distribution of the light organs, by size groups, has been plotted (Fig. 5), in order to obtain a clearer comparison of the three samples. The two Indo-Pacific samples look as though they were reasonably homogeneous, but the plot of the Atlantic sample gives the impression that it may be composed of two groups. One, the more numerous, has a mean value somewhere around five; the other, with a greater range, looks to have a mean in the neighborhood of nine. But we are still unable to find any means of separating out two groups from this single distribution. A scatter diagram of the size of the organ of the first row plotted against the size of the organ of the

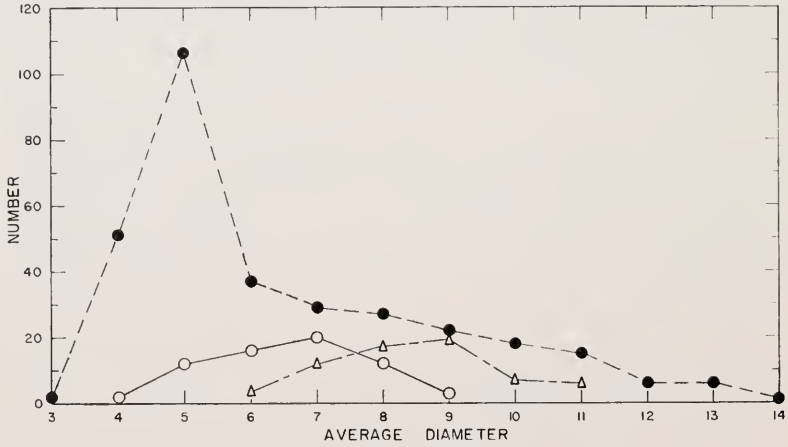

Figure 5. Frequency diagram of the distribution of the diameters of the first row organs. Solid circles — *C. sloani* from the Atlantic. Open circles — *C. sloani* from the Indo-Pacific. Triangles — *C. sloani secundus.*

fifth row (Fig. 6) shows in a rather striking fashion that there is actually no real reason for attempting to make such a separation. There appears to be a general increase in the size of one organ with the size of the other, but over so broad a base that it is difficult to draw any hard and fast conclusions on this matter.

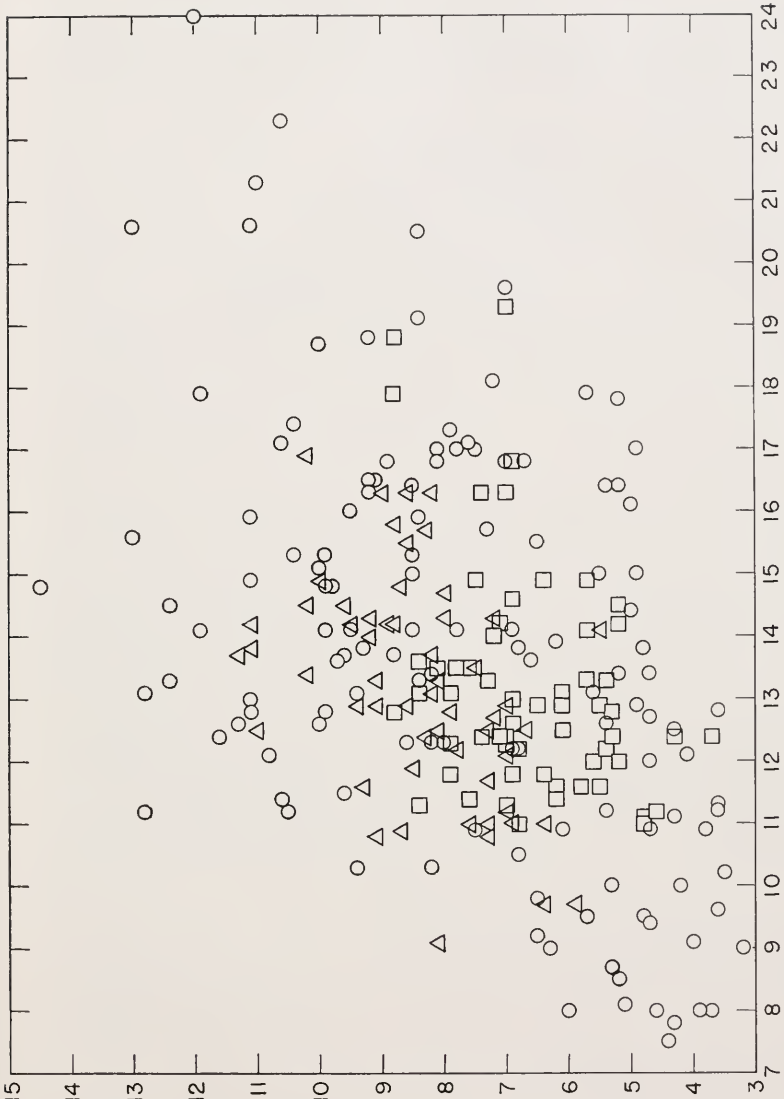

Figure 6. Scatter diagram of size of light organs of fifth scale row (abscissa) and of first row (ordinate) as percentages of average diameter of scales of second row. Circles — *C. sloani* from Atlantic. Squares — *C. sloani* from Indo-Pacific. Triangles — *C. sloani secundus*.

Further, the measurements of the organs of Indo-Pacific *C. sloani* and of *C. sloani secundus* fall entirely within the scatter of the Atlantic specimens of *C. sloani*. We are thus reinforced in our conclusion that *C. sloani secundus* should not be considered as a subspecies.

The number of serial photophores in the lateral and ventral series is an extremely valuable characteristic on which several species may be distinguished. In particular, *C. schmidti* and *C. pammelas* have much lower counts than any other species except *C. barbatus,* but they are readily distinguished from *C. barbatus* on other grounds. *C. pammelas,* with only 58 to 61 ventral organs and 38 to 39 lateral ones, falls completely outside the range of *C. sloani* for this character. For this reason we do not hesitate to consider *C. pammelas* as a species completely distinct from *C. sloani*. There seems to be no justification for maintaining *C. pammelas* as a subspecies of *C. sloani*. The matter of *C. schmidti* as a species or as a subspecies of *C. sloani* is not quite as clear cut, for there is some degree of overlap between the highest counts of *C. schmidti* and the lowest counts of *C. sloani*. Confining the discussion of the Atlantic forms of *C. sloani,* we find that this species has a total count of organs in the ventral row of 63 to 70. In the lateral row, the count is 42 to 48. For *C. schmidti,* the corresponding values are 60 to 63 and 38 to 42. But we must point out that in the ventral row counts, the number of *C. sloani* that overlap the range of *C. schmidti* is 3 out of a total of 298 specimens. (We have here included data on 197 specimens published by Ege (1948) and 101 specimens examined by us.) For the 54 specimens of *C. schmidti* reported by Ege, 14 had 63 photophores in the ventral row, 40 had 60 to 62. The coefficient of difference for the two distributions is 2.09, far above the usual subspecific level and indicating a much greater degree of differentiation. The same conclusion must be drawn from the graphic presentation of the statistics of these data, shown in Figure 7. The ranges of the two distributions meet at the value 63, but the two standard deviations are separated by a distance equal to 1.6 times larger. We feel completely justified, then, in raising *C. schmidti* to specific rank.

Two other items must be mentioned in this section. One of these is the shape and location of the postocular photophore, a characteristic which, as far as we know, has not previously been utilized in this group. In all species except *C. macouni,* this organ is more or less round and located generally somewhat anterior to a vertical through the posterior margin of the eye.

In *C. macouni,* however, the organ is generally triangular and pointed behind, sometimes notably elongate, and is placed posterior to the vertical through the hind border of the eye.

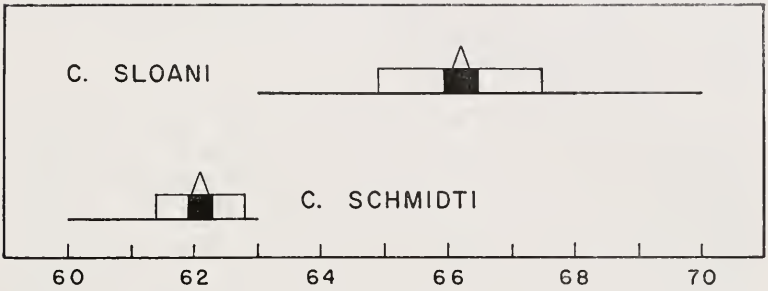

Figure 7. Distribution of the total number of serial photophores in the ventral row in two species of *Chauliodus.*

The other characteristic is the structure of the barbel. This was mentioned briefly by Regan and Trewavas (1929), but appears to have been ignored by most other workers. As Regan and Trewavas pointed out, the barbel of *C. sloani* is tapered and flexible, and disappears at a rather early age. This appears to be true also of *C. schmidti* and *C. pammelas.* In *C. danae* and *C. barbatus,* the barbel is stiff and compressed. In *C. danae,* the organ is quite straight, without expansions, and has degenerated in most specimens larger than 50 mm standard length. In *C. barbatus,* by contrast, the barbel bears a terminal, leaf-like expansion, and the whole organ is retained even in the largest specimens. In *C. macouni* the barbel resembles that of *C. sloani,* but is longer, stiffened basally, and does not degenerate.

DEFINITIONS

Two terms that have been and will be used in this paper require definition, as they are not ordinarily found in descriptions of fishes.

Scale areas. These are actually the scale pockets. (For a detailed description, see Morrow, Chauliodontidae, Fishes of the Western North Atlantic, Vol. 3.) The scales of *Chauliodus* are large and fairly heavy. However, they are extremely deciduous, and appear also to dissolve readily in the ordinary preserving fluids. In addition, the skin is, in life, covered with a thick layer of mucus which makes it very difficult to distinguish the scales themselves. Each scale pocket is outlined by a pigment pattern,

so that even after the scales are lost, the areas can often be distinguished with a fair degree of ease and accuracy. In the terminology used here, the most dorsal row of scales is called the first row. The scales of this row are much smaller than the others, and are often almost impossible to see. The most ventral row of scales is termed the fifth row.

SM organs. These are the small light organs lying in the area between the lateral and ventral rows of serial light organs. The arrangement of these small organs is here indicated by a numerical formula showing the number of small, unpigmented organs at each end and the number of somewhat larger pigmented organs in the middle of the series between adjacent pairs of large, serial photophores. Thus, 1+3+0 would indicate one small unpigmented organ at the anterior end of the series, three larger, pigmented organs in the middle part, and no organ at the posterior end.

All descriptions of scale areas and SM organs refer to the part of the body beginning four or five scales behind the bases of the ventral fins and extending posteriorly for about ten scales.

Family CHAULIODONTIDAE

Characters. Body long, slender, compressed, covered by five longitudinal rows of large scales. Scales deciduous, their location often marked only by pigment pattern. Ventral fins before middle of body measured from snout, of seven or eight rays. Dorsal fin in anterior third of body, far in advance of anal fin, its first ray much produced into a long filament, terminating in a small flap. Adipose dorsal and anal fins present. Anal fin far posterior, close to caudal.

Premaxillaries not protractile. Well developed epiotics present beside supraoccipital. Parietals minute. First few vertebrae without centra, the notochord enclosed in a sheath, first vertebra with a large single parapophysis below, and long paired laminae above representing neural arch. The enlargement of this vertebra, together with the acentrous nature of the ones behind it, is related to throwing back the head in order to open the mouth in feeding (Tchernavin, 1953). The remainder of the skeleton is much like that of the Astronesthidae, and is but poorly ossified.

Snout short, more or less equal to eye. Nostrils large, immediately before eyes, the complex olfactory laminae exposed. Interorbital less than eye, with a prominent bony ridge above each eye. Teeth of premaxillary and mandible rigid, large to enormous,

fang-like. Mandible with none to many tiny denticles near rictus. Maxillary with numerous fine teeth on posterior half to two-thirds of its ventral margin, entering posterior portion of gape. Vomer toothless. Palatines with a few teeth anteriorly, followed by a space, then several minute teeth. Operculum small. Four gills, a slit behind the fourth. Gill arches armed with teeth, but no true gill rakers. Mental barbel generally short and simple, becoming much reduced or absent in juveniles and adults of some species, retained in others.

Postocular luminous organ present, below and just before or somewhat behind posterior margin of eye, another organ imbedded in skin immediately before eye. Small photophores present in each scale area. A row of large light organs present on each side of body, beginning immediately behind gill opening and ending above or nearly above anterior end of anal fin. Another row of large photophores below these, beginning at anterior end of isthmus and ending at caudal base. Between the two rows of large organs is a wavy row of small ones (here termed SM organs), whose pattern more or less repeats itself between each pair of large serial organs, and appears to be diagnostic for some species. Groups of small organs present on mid-ventral line between the two ventral rows of large photophores. Light organs present on branchiostegal membranes, between rays.

Miscellaneous anatomy. The internal anatomy of the major systems is typical of pelagic teleosts, with minor adaptations in the digestive system which are presumably related to the availability of food in the mid-depths. It has been examined in detail by Haffner (1952a), whence most of the following account has been derived.

The most prominent feature of the digestive tract is the long, sac-like stomach. Apparently it is not particularly distensible, but achieves its capacity through its length. As with other pelagic fishes, the esophagus, intestine and pyloric caeca join the stomach at its anterior end.

The esophagus is muscular, lined with short columnar epithelial cells, some of which, in the anterior portion, have a short, curved spine at their free end. The spines disappear in the posterior portion of the esophagus, and their function is unknown. In the anterior portion of the stomach, the mucosal lining is thrown into folds, with each fold bearing a lymph nodule at its tip. The pyloric caeca are thin-walled, and the mucosa and submucosa are much folded, resulting in the division of each caecum into

numerous small compartments. Haffner suggested that the compartments were so small as to prevent the entrance of food into them, and hazarded that the caeca might be secretory in function. The intestine, arising on the ventral side of the stomach at its anterior end, extends straight back to the anus with no change in diameter.

The kidneys are long and narrow, extending the full length of the body cavity, and appear to be aglomerular. The urinary bladder opens through a pore behind the opening of the genital duct. The gonads resemble the kidneys in gross appearance, but do not reach as far posteriorly. The genital ducts empty through a pore between the anus and the urinary pore.

The swim bladder, according to Marshall (personal communication of information in press), is either absent, or degenerates completely at a very early stage.

The microscopic structure of the photophores has been the subject of several investigations, (Chiarini, 1900; Brauer, 1908; Haffner, 1952a), with the result that they have been thoroughly described and illustrated. There are four types, the simplest being merely a small, spherical mass of radially-arranged columnar cells, without pigment layer, lens, or reflector. The next form, of which the sub-ocular photophore is typical, also lacks lens and reflector, but is provided with a layer of dark pigment covering about ¾ of its surface. Its structure resembles that of the simplest type, except that instead of a lumen, the center of the organ is filled with what Brauer interpreted as coils of cells, but which Haffner thought could be explained more readily as the cut ends of radially-arranged columnar cells. The more complex organs, consisting of light-producing elements, pigment layer, lens and reflector, are of two types, the bowl and cup-shaped organs, and the bell-shaped organs. The former have a single, the latter a double lens.

The photophores were early thought to be equipped with nerve fibers, but later workers have interpreted the observed structures as blood vessels, indicating that the luminescence of the photophores is under hormonal rather than direct nervous control.

Range. The several species of *Chauliodus,* the only genus of the family, are found in nearly all parts of the oceans, having been taken throughout the North Atlantic and Mediterranean, at various localities in the South Atlantic, and in the Pacific and Indian oceans. In general, the range lies between 50°N and 40°S, although *C. macouni* is commonly found in the Gulf of Alaska to

60°N, and there are few records of *C. sloani* in the Atlantic between 55°N and 65°N.

In their vertical distribution, the members of this group may be found as close to the surface as 20 meters, and down to depths as great as 2,800 meters. Several species appear to have different depth preferences, and all appear to be more or less limited in their distribution by certain physical and chemical characteristics of the water masses. In general, larger individuals, and also species reaching larger sizes, tend to live at greater depths than do the smaller ones.

Genus CHAULIODUS Bloch and Schneider, 1801

Chauliodus Bloch and Schneider, Systema Ichthyologiae, Berlin, 1801: 430; type species *C. sloani* Bloch and Schneider, 1801, by monotypy.

Generic Synonym:

Leptodes Swainson, Nat. Hist. Classification Fishes, Amphibians and Reptiles. London, 1839: 298; type species *L. sloanii* (Bloch and Schneider).

Generic characters. As for the family.

Size and habits. The various species included in *Chauliodus* are of no more than moderate size. *C. sloani* has been recorded at a length (standard or total?) of 350 mm (Zahl, 1953), but the vast majority of individuals do not appear to exceed about 300 mm standard length. *C. danae*, in particular, does not appear to reach more than about half this length.

The habits of this group, are, of course, unknown from direct observation, but examination of stomachs of preserved individuals has shown them to be carnivores, feeding on other fishes and on crustaceans. Tchernavin (1953) has deduced the detailed mechanics of their feeding actions from a study and dissection of *C. sloani*. Larval development of *C. sloani* has been described, but that of other species remains unknown. (For a résumé, with many references, of current knowledge of larval development in *Chauliodus,* see Morrow, Fishes of the Western North Atlantic, vol. 3.)

Species. All told, some 14 names, which do not include combinations, have been applied to the members of the genus *Chauliodus,* but no one has ever attempted to accept all fourteen as valid. The first attempt to list the species seems to have been that of Garman (1899), who recognized five, but made no indication of his thoughts on the remaining three which had been described

at that time. Brauer (1906) considered the matter in more detail and accepted the same five species. He also pointed out that *C. setinotus* Bloch and Schneider and *C. schneideri* Risso were synonyms of *C. sloani* Bloch and Schneider. Regan and Trewavas (1929) gave detailed descriptions of their material of three species and suggested that *C. dannevigi* and *C. macouni* might be synonyms of *C. sloani* and *C. barbatus*, respectively. Finally, Ege (1948) accepted only *C. sloani*, *C. danae* and *C. barbatus* as full species, reducing *pammelas, dannevigi* and *macouni* to subspecies of *sloani* and describing two new subspecies, *schmidti* and *secundus*. Thus, he considered that there were three species, one of which was split into six subspecies, for a total of eight forms.

In the present paper, we recognize six species. The subspecies of Ege we feel should either be raised to specific rank or synonymized altogether, as has already been pointed out in the section on species criteria.

Key to Species

1a. Postocular photophore elongate, the exposed luminous portion triangular or at least pointed behind; the organ itself located below or behind a vertical through posterior edge of eye.

C. macouni Bean
Gulf of Alaska, North Pacific Ocean

1b. Postocular photophore round or nearly so, exposed luminous portion never triangular or pointed behind; the organ itself located below or before a vertical through posterior edge of eye.

2a. Serial photophores of lateral series ventral to scale areas of fourth row. Majority of scale areas of 3rd row generally with a cluster of 3 or more small light organs.

C. barbatus Garman
Gulf of Panama, tropical Pacific

2b. Serial photophores of lateral series below scale areas of fifth row. Scale areas of 3rd row with not more than 2 small light organs.

3a. Dorsal origin over 9th to 12th OV photophore.

4a. Posterior unpigmented organ of each SM series generally absent, or at least much reduced. SM formula generally 1+2+0. Chin barbel (when present) short, stiff, compressed,

absent in most specimens larger than ca 50 mm.
C. danae Regan and Trewavas
North and South Atlantic Ocean.

4b. Posterior organ of each SM series nearly as large as the central organs. SM formula generally 1+3+1 or 1+4+0. Barbel tapered, slender, flexible, generally present in most specimens up to ca 100 mm.
C. sloani Bloch and Schneider
(some Indo-Pacific variants)

3b. Dorsal origin over 5th to 8th OV photophore.

5a. Total ventral photophores 64 to 72, rarely 62 or 63. Total lateral photophores 43 to 48, rarely 42.
C. sloani Bloch and Schneider
Atlantic, Pacific, Indian oceans, Mediterranean Sea.

5b. Total ventral photophores 58 to 63. Total lateral photophores 38 to 42.

6a. SM series with 3, sometimes 4 larger pigmented organs in each series. Total ventral organs 58 to 61, total lateral organs 38 to 39.
C. pammelas Alcock
Northern Indian Ocean

6b. SM organs with only 2 larger pigmented organs in each series. Total ventral organs 60 to 63, total lateral organs 38 to 42.
C. schmidti Ege
Eastern Atlantic Ocean

Chauliodus barbatus Garman, 1899

Study material. Nineteen specimens, 74 to 183 mm standard length, from the Gulf of Panama, Galapagos Islands and off Peru.

Distinctive characters. C. barbatus is particularly characterised by the following: Serial photophores of the lateral series located on verticals passing approximately through the centers of the scale areas of the fourth row; barbel stiff, compressed, expanded at tip, present at all stages; dorsal origin over 8th to 11th OV photophore; total lateral photophores 38-41; total ventral photophores 59-63.

Description. Proportional measurements of the study material given as average percentages of standard length except as indicated otherwise, with the range of variation shown in parentheses.

Body: depth 9.9 (7.1-14.8).

Head: 15.3 (13.5-16.5).

Eye: 3.1 (2.6-3.4); 20.1% of head (17.0%-22.3% of head).

Snout: 3.5 (3.1-4.1); 22.6% of head (19.5%-26.0% of head).

Distance from snout: to origin of dorsal fin 27.0 (25.1-29.0); to origin of anal fin 81.7 (79.0-83.1); to origin of ventral fin 41.9 (40.5-44.1).

Pre-anal length without head: 66.5 (63-69).

Dorsal fin: rays 6.

Anal fin: rays 10-13.

Pectoral fin: rays 10-13.

Ventral fin: rays 7.

Vertebrae: 51-55, most often 53.

Serial photophores: Ventral row: IP 9-11; PV 16-19; VAV 22-24; AC 10-11; Total 59-63. Lateral row: OV 17-18; VAL 20-23; Total 38-41.

Body elongate, slender, compressed, the depth averaging about 10 per cent of the standard length, slightly deeper than in other species. Barbel present at all stages, short, stiff, compressed, terminally expanded. Edges of expanded part usually crenate (Fig. 8).

Head about $\frac{1}{7}$ of standard length, with prominent bony ridges above each eye. Eye round, about $\frac{1}{5}$ of head. Snout slightly longer than eye diameter. Subocular organ present below anterior part of eye, deeply embedded in skin. Postocular organ more or less round, located below posterior part of eye.

Mouth large, jaws almost equal to head length. Premaxillaries with four teeth, second tooth longest, third tooth longer than (rarely equal to) fourth. Many small oblique teeth on maxillary. Mandible with 6 to 9 larger teeth, and up to 5 tiny dentieles posteriorly, near corner of mouth.

Origins of pectoral fins low on body, just anterior to posterior edge of opercular flap when head is in normal position. Fins of 10 to 13 rays. Ventral fins of 7 rays, their origins before middle of standard length. Dorsal fin of 6 rays, its origin over the 8th to 11th OV photophore. Anal fin far behind dorsal, close to caudal, with 10 to 13 rays, most often 12 or 13. Caudal fin forked.

Scale areas of the second row almost always, and of the fourth row usually, with only one small light organ. Areas of the third

row with a cluster of three or more small organs, usually one slightly larger and two to many rather minute ones. Serial photophores lying below scales of fourth row, scales of fifth row extending ventrally between the organs of the lateral row. SM organs small, usually five to seven of about equal size in each section.

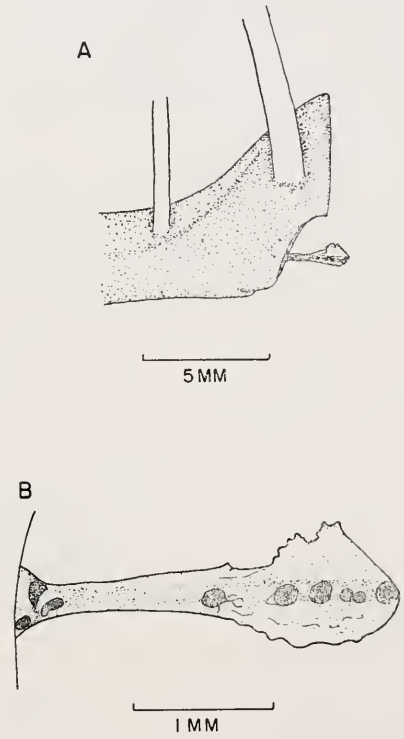

Figure 8. Barbel of *C. barbatus* Garman, drawn from Galathea specimen No. 15. A) Showing relation to lower jaw. B) The barbel itself, much enlarged.

Size. The largest specimen examined was 183 mm in standard length. It seems likely that this species does not much exceed 200 mm.

Relationships. C. barbatus clearly represents an individual offshoot within the genus. Although the stiff compressed barbel suggests affinities with *C. danae*, and the retention of the barbel throughout life is found also in *C. macouni*, the arrangement of the serial light organs below the fourth, rather than the fifth,

scale row, the presence of a group of organs rather than a pair in the areas of the third row, and the increased number and reduced size of the SM organs all indicate that *C. barbatus* is the most divergent species of the genus.

Range. Known only from the eastern part of the Pacific Equatorial water mass, from the coast of Peru north to the Gulf of Panama (possibly as far north as Central America) and westward to about 100°W. In depth, *C. barbatus* has been taken down to about 1200 fathoms, but the majority of records seem to be from between 500 and 700 fathoms.

Synonyms and references:

Chauliodus barbatus Garman, Mem. Mus. Comp. Zool. Harvard, *24,* 1899: 271-273, Pl. K, figs. 2, 2a (type descr., illus., type localities 6°22′20″N, 81°52′W, 465 fath., and 3°09′N, 82°08′W, 1132 fath., type specimens, Harvard Mus. Comp. Zool., Nos. 28489 and 28490); Brauer, Ergebn. Deutsch. Tiefsee-Exped. "Valdivia", *15,* Syst. Teil, 1906: 38-40 (comparison species); Gilbert, Proc. U.S. Nat. Mus., *48,* 1915: 321 (name); McCulloch, Biol. Res. "Endeavour", 1916, *4* (4): 181 (name); Regan and Trewavas, Dana Rept., No. 5, 1929: 38-39 (descr., Gulf of Panama); Jordan, Evermann and Clark, Rep. U.S. Comm. Fish., (1928) 1930, App. X: 71 (name); Ege, Dana Rept., No. 31, 1948: 148 pp. (descr., synonymy, zoogeogr.); Haffner, Syst. Zool., *1* (3), 1952: 114 (name, Gulf of Panama to Galapagos); Marshall, Aspects of Deep Sea Biology, New York, 1954: 65 (name).

Chauliodus danae Regan and Trewavas, 1929

Study material. Seventy specimens 37 to 133 mm standard length, from the Caribbean Sea and North Atlantic Ocean.

Distinctive characters. The posterior position of the dorsal origin, the short stiff barbel of the young, and the reduced SM organs serve to distinguish *C. danae.*

Description. Proportional measurements of the study material expressed as mean percentages of standard length except as noted otherwise, with the range of variation shown in parentheses. Data from other authors in brackets.

Body: depth 7.7 (4.7-11.9).

Head: 12.9 (11.9-14.3).

Eye: 3.3 (2.2-4.9); 26.9% of head (17.7%-43.2% of head).

Snout: 2.8 (1.7-3.7); 22.3% of head (16.7%-28.8% of head).

Distance from snout: to origin of dorsal fin 28.1 (25.9-32.3); to origin of anal fin 85.7 (83.5-88.7); to origin of ventral fin 42.7 (39.7-45.7).
Pre-anal length without head: 73 (71-77).
Dorsal fin: rays 6.
Anal fin: rays 10-12.
Pectoral fin: rays 12-13 [14].
Ventral fin: rays 7.
Vertebrae: 51-57, most often 53-55.
Serial photophores: Ventral row: IP 9-10; PV[17]18-21; VAV[22]23-26; AC 8-10; Total 61-65. Lateral row: OV 17-20; VAL 22-25; Total 40-44.

Body compressed, elongate, slender, the depth averaging only about 1/15 of the standard length. Barbel present only in young (less than ca 50 to 55 mm SL), compressed, straight, with a stiffening axial rod, reduced to a small triangular stump in adults. (Fig. 9.)

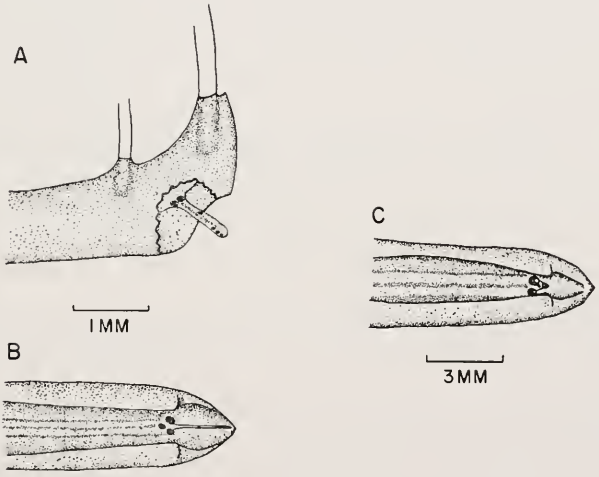

Figure 9. Barbels of *C. danae.* A) Lateral view, with part of lower jaw cut away, of barbel of a 50 mm specimen (Bingham Oceanogr. Coll., No. 2938). B) Ventral view of same. C) Ventral view of barbel of a 114 mm specimen (Bingham Oceanogr. Coll., No. 2935) showing reduction in adult.

Head averaging about 1/8 of standard length, bony ridges present above eyes. Eye round, its diameter quite variable, generally somewhat larger in males than in females (Regan

and Trewavas, 1929: 34). Snout slightly shorter than eye diameter. Subocular organ present below front of eye, deeply embedded. Postocular organ round, below posterior part of eye.

Mouth large, jaws almost equal to head length. Premaxillaries with four teeth, second longest, third tooth shorter than (rarely about equal to) fourth. Many small, oblique teeth on maxillary. Mandible with 5 to 11 teeth, generally 7 or 8, with up to 8 denticles posteriorly near corner of mouth (see Table IV).

Pectoral fins with 12 to 14 rays, their origins low on body, about below posterior edge of opercular flap. Ventral fins with 7 rays, their origins before middle of standard length. Dorsal fin of 6 rays, its origin generally over 9th to 11th OV photophore, rarely 8th or 12th. Anal fin far behind dorsal, close to caudal, with 10 to 12 rays. Caudal fin forked.

Scale areas generally clearly marked by pigment patterns, each area with one or more small light organs, those of the third row with not more than two photophores. Areas of second and fourth rows each with two organs. Serial photophores lying below scales of fifth row. SM organs generally with the posterior organ of each section absent or at least much reduced, the SM formula 1+2+0.

Size. The largest specimen seen by us was 133 mm in standard length. According to Regan and Trewavas (1929: 35), the maximum size is about 140 mm.

Relationships. Closest to *C. sloani*, from which it differs chiefly in the structure of the barbel, the posterior placement of the dorsal fin, the reduced SM organs and the somewhat lower number of serial photophores.

Range. The majority of the known specimens of *C. danae* have come from a broad east-west belt across the North Atlantic, extending roughly from 20°N to 40°N. However, other specimens have been recorded from the South Atlantic, as far as 33°53′45″S, and from as far north as 51°N. In addition, the species has also been recorded from the area along the eastern edge of the Caribbean Sea and from the Yucatan Channel, west of Cuba. Within these areas, it appears that *C. danae* is restricted to water in which the degree of oxygen saturation is at least 50 per cent. Depthwise, *C. danae* has been recorded as far down as about 3500 meters (7000 meters of wire out), but the majority of specimens appear to be taken in the upper 500 meters of water.

Synonyms and References:

Chauliodus danae Regan and Trewavas, Dana Rept., No. 5, 1929; 34-38, pl. VII (type descr., type locality 13°03'N, 59°50'W, 300 m wire, type specimen Dana Coll. No. St. 1182); Norman, Discovery Rept., *2*, 1930: 308 (South Atlantic); Borodin, Bull. Mus. Comp. Zool. Harvard, *72* (3), 1931: 64 (Bermuda); Fowler, Bull. Amer. Mus. Nat. Hist., *70* (2), 1936: 1199-1200 (name); Beebe, Zoologica, N.Y., *22* (14), 1937: 201 (Bermuda, 300-1,000 fath.); Parr, Bull. Bingham Oceanogr. Coll., *3* (7), 1937; 58 (Bahamas, Bermuda); Bertin, Bull. Mus. Hist. Nat. Paris, (2) *11*, 1939: 382 (name); Nybelin, Göteborg Vetensk. Samh. Handl., (B) *5* (16), 1948: 30 (N.E. Atlantic); Ege, Dana Rept., No. 31, 1948: 1-148 (classification, phylogeny, zoogeography); Haffner, Systematic Zool., *1*, (3), 1952: 112-113 (zoogeography); Grey, Fieldiana:Zool., *37*, 1955: 277-278 (Bermuda, stomach contents, eggs); Koefoed, Rep. Sars N. Atlantic Deep Sea Exped., *4* (2) (5), 1956: 19-20 (N. Atlantic, table of measurements).

Chauliodus atlantis (partim) Barbour, Proc. New Engl. Zool. Cl., *19*, 1942: 46.

Probable synonym:

Chauliodus pammelas Pappenheim, Deutsch. Südpolar Exped., *15*, Zool. *7*, 1914: 167 (N. Atlantic).

Not *Chauliodus danae* Phillipps, Rec. Dominion Mus., *1* (1), 1942: 53-54 (Cook Strait).

Chauliodus macouni Bean, 1891

Study material. Ninety-three specimens, 30 to 182 mm standard length, from the northeastern Pacific Ocean and south of Japan.

Distinctive characters. The generally triangular form of the postocular organ, and its location behind and below the eye provide absolutely distinctive characters by which to distinguish *C. macouni* from all other species of the genus.

Description. Proportional measurements of the study material expressed as average percentages of standard length, unless indicated otherwise, with the range of variation shown in parentheses. Data in brackets from other authors.

Body: depth 8.1 (6.7-10.1).

Head: 15.8 (13.2-17.2).

Eye: 3.3 (2.8-4.0); 20.8% of head (16.9%-28.1% of head) [30.3].

Snout: 3.8 (2.8-4.5); 24.4% of head (17.7%-28.7% of head) [30.3].
Distance from snout: to origin of dorsal fin 24.9 (22.2-27.8); to origin of anal fin 83.3 (80.9-84.7) [76.8-90.8]; to origin of ventral fin 41.3 (37.6-44.5) [35.7-47.5].
Pre-anal length without head: 68 (64-72).
Dorsal fin: rays 6 [rarely 7].
Anal fin: rays 10-13.
Pectoral fin: rays 10-13.
Ventral fin: rays 7 [rarely 8].
Vertebrae: 56-62.
Branchiostegal rays: 16-20 [21].
Serial photophores: Ventral row: IP 9-12; PV 17-21; VAV 26-29 [30]; AC 10-13; Total 66-69. Lateral row: OV 17-20; VAL 24-28 [29]; Total 43-46.

Body slender, elongate, compressed, its depth averaging about 1/12 of the standard length. Barbel rather longer than in other species, tapered, stiff basally but flexible near tip, present at all stages (Fig. 10).

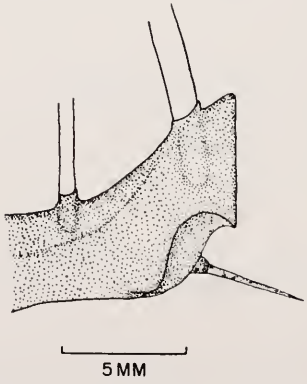

Figure 10. Barbel of *C. macouni*. Drawn from Bingham Oceanogr. Coll., No. 1287, 159 mm standard length.

Head almost 1/6 of standard length, with the usual bony ridges above eyes. Eye round, its horizontal diameter averaging about 1/5 of head. Snout generally a little longer than eye. Subocular organ present below and before eye, deeply embedded. Postocular organ located generally behind a vertical through posterior margin of eye, the organ itself distinctly

elongate, the exposed luminous surface generally markedly triangular or at least pointed behind, sometimes notably attenuate.

Mouth large, jaws almost equal to head. Premaxillaries with four teeth, second largest, third tooth longer than (rarely equal to) fourth. Many small, oblique teeth on posterior part of maxillary, which enters gape. Mandible with five to nine larger teeth, generally six or seven. Usually no dentieles on posterior part of mandible, but sometimes as many as four present. (See Table IV.)

Pectoral fins arising low on body, below posterior edge of opercular flap, of 10 to 13 rays. Ventral fins of 7 rays, arising well before middle of standard length. Dorsal origin over 6th to 9th OV photophore, average predorsal distance about ¼ of standard length. Anal fin far behind dorsal, close to caudal, of 10 to 13 rays. Caudal fin forked.

Body with five longitudinal rows of scales, large serial photophores of lateral row lying below scales of fifth row. Scale areas of second row generally with only a single light organ, those of third row with two, those of fourth row usually with one photophore. SM organs generally 0+2+1, but showing considerable variation, sometimes 1+4+0, the latter formula found in the type specimen and a few others.

Size. The largest specimen examined, at 182 mm SL, appears to be the longest on record, suggesting that this species may not ever grow to much over about 200 mm SL.

Relationships. C. macouni appears to be closer to *C. sloani* than to any other species in the genus, although the long third tooth of the premaxillary and the permanent nature of the chin barbel indicate affinities with the stock from which *C. barbatus* must have arisen.

Range. The vast majority of records of *C. macouni* have come from the subarctic Pacific water mass and the intermediate water to the west of it, with a few from the transitional region that extends south along the California coast. There are a few records from other masses, e.g., one from the Pacific Equatorial Water near the Galapagos Islands and another from south of Japan in the border region between Intermediate and Western North Pacific Central Water, but it is quite possible that these were strays and that these records do not really represent the normal extension of the range. Present information, then, suggests that the ordinary range of *C. macouni* includes the southern part of the Bering Sea, southeastward through the Gulf of

Alaska at least as far as the southern part of California, and westward about to Sakhalin, possibly as far as Japan.

Synonyms and references:

Chauliodus macouni Bean, Proc. U.S. Nat. Mus., *13*, (1890) 1891: 44 (type descr., type locality 51°23′N, 130°34′W, 876 fath., type specimen U.S. Nat. Mus., No. 45372); Gilbert, Rept. U.S. Comm. Fish., (1893) 1895: 402 (off Oregon, Alaska); Goode and Bean, Oceanic Ichthyol., Washington, 1895: 513 (name); Jordan and Evermann, Bull. U.S. Nat. Mus., *47*, 1896: 585 (descr.); Garman, Mem. Mus. Comp. Zool. Harvard, *24*, 1899: 274 (name, meristic counts); Brauer, Ergebn. Deutsche Tiefsee-Exped. "Valdivia", *15* Syst. Teil., 1906: 38-40 (comparison other spp.); Gilbert, Proc. U.S. Nat. Mus., *48*, 1915: 321-322 (descr., comparison other spp., So. Calif.); McCulloch, Biol. Res. "Endeavour", *4* (4), 1916: 181 (name); Jordan, Evermann and Clark, Rep. U.S. Comm. Fish., (1928) 1930, App. X: 71 (name); Chapman, Occ. Pap. B. C. Prov. Mus., No. 2, 1940: 5-11 (distrib., descr., comparison *C. barbatus*); Clemens and Wilby, Bull. Fish. Res. Bd. Canada, *68*, 1946: 108-109 (descr., illus., food, range); Barraclough, Copeia, 1950 (3): 241-242 (inshore record, Brit. Columbia); Copeia, 1954 (1): 75-76 (same).

Chauliodus emmelas Jordan and Starks, Bull. U.S. Fish. Comm., *22*, 1904: 579 (type descr., type locality Sagami Bay, Japan, 120-265 fath., type specimen U.S. Nat. Mus., No. 51464); McCulloch, Biol. Res. "Endeavour", *4* (4), 1916: 181 (name).

Chauliodus sloanei macouni Ege, Dana Rept., No. 31, 1948: 148 pp. (descr., near Galapagos Is.); Haffner, Systematic Zool., *1* (3), 1952: 114, 132 (name, range).

Chauliodus pammelas Alcock, 1892

Study material. Seven specimens, 25 to 159 mm standard length, from the Gulf of Aden, Arabian Sea and near the Maldive Islands.

Distinctive characters. C. pammelas is set off primarily by the low number of serial photophores, the forward position of the dorsal fin, and the 3 or 4 pigmented SM organs.

Description. Proportional measurements of the study material as mean percentages of standard length, unless indicated otherwise, with range of variation in parentheses.

Body: depth 8.5 (7.2-9.5).

Head: 15.1 (14.0-16.5).
Eye: 3.3 (2.8-4.4); 21.6% of head (19.1%-23.4% of head).
Snout: 3.5 (3.1-4.4); 22.3% of head (20.6%-25.1% of head).
Distance from snout: to origin of dorsal fin 23.2 (21.5-26.7); to origin of anal fin 83.5 (82.5-84.5); to origin of ventral fin 43.8 (41.5-45.3).
Pre-anal length without head: 67.9 (63-70).
Dorsal fin: rays 6.
Anal fin: rays 12-13.
Ventral fin: rays 7.
Pectoral fin: rays 12-14.
Vertebrae: 50-53.
Branchiostegal rays: 17-20.
Serial photophores: Ventral row: IP 10; PV 17-19; VAV 21-23; AC 9-11; Total 58-61. Lateral row: OV 18-19; VAL 19-22. Total 38-39.

Body, slender, elongate, compressed, depth about 1/12 of standard length. Chin barbel reduced to triangular stump in study material.

Head 1/6 to 1/7 of standard length, a bony ridge above each eye. Eye round, average diameter a little more than 1/5 of head, averaging slightly less than snout length. Snout short, less than ¼ of head. Subocular organ present below front of eye, deeply embedded in skin. Postocular organ round, below eye, before a vertical through posterior margin of eye.

Mouth large, jaws nearly equal to head length. Premaxillaries with four teeth, second tooth longest, fourth tooth longer than third. Maxillaries with numerous small, oblique denticles on posterior part of ventral margin, entering gape. Mandible with five teeth, and up to 17, perhaps more, tiny denticles near corner of mouth. The number of denticles appears to be a function of the size of the individual, increasing as the fish grows.

Origins of pectoral fins low on body, about below posterior edge of opercular flap. Fins of 12 to 14 rays. Ventral origins before middle of standard length, close together at mid-ventral line. Dorsal fin arising over 6th or 7th lateral OV photophore, pre-dorsal distance 21.5 to 26.7 per cent of standard length. Anal fin far behind dorsal, close to caudal, with 12 or 13 rays. Caudal fin forked.

Body with five longitudinal rows of scales, the scale areas marked off by pigment patterns. Second row with one or (more

often) two small organs in each scale area. Each area of third row with only two small light organs, areas of fourth row also with two organs. Serial photophores ventral to scale areas of fifth row. SM organs moderate, SM formula usually 0+3+1, sometimes 0+4+0.

Size. The type specimen, described by Alcock (1892: 355) as "10 inches long," is the largest of which we have found a record.

Relationships. C. pammelas is obviously derived from the *sloani* stock, and appears to occupy a position close to *C. schmidti* of the Atlantic, which it resembles, especially in the low number of serial photophores. Whether the ecological positions are similar is not known.

Range. This species has been recorded from the Gulf of Aden, eastwards across the Arabian Sea to the Maldive-Laccadive area, south and west of Ceylon, in the Bay of Bengal and southwest of the Nicobar Islands, and once from the Flores Sea. The last is the only record ascribed to this species south of the equator. The depth range apparently goes to something on the order of 2500 meters, with several other positive records between 500 and 1000 meters, approximately. Unfortunately, this species is not particularly abundant in collections, and its distribution is therefore not well known.

Synonyms and references:

Chauliodus pammelas Alcock, Ann. Mag. Nat. Hist., (6) *10,* 1892: 355 (type descr., type locality Laccadive Sea, 8°49′N, 73°18′45″E, 1370 fath., type specimen Indian Mus. No. 13183); Goode and Bean, Oceanic Ichthyol., Washington, 1895: 96 (name); Alcock, Descr. Cat. Indian Deep Sea Fishes, Calcutta, 1899: 145 (not seen); Illus. Zool. "Investigator," 1900: Pl. 30, fig. 4 (not seen); Brauer, Ergebn. Deutsche Tiefsee-Exped. "Valdivia", *15* Syst. Teil, 1906: 38-42 (comparison other spp.); 42-43 (descr.); Weber and de Beaufort, Fishes Indo-Austral. Archipel., Leiden, vol. 2, 1913: 110-111 (name); McCulloch, Biol. Res. "Endeavour", *4* (4), 1916: 181 (name); Regan and Trewavas, Dana Rept., No. 5, 1929: 31 (name); Fowler, Bull. Amer. Mus. Nat. Hist., *70* (1), 1936: 221 (name); Norman, Sci. Rept. John Murray Exped., *7* (1), 1939: 21-22 (descr., distrib.).

Chauliodus sloanci pammelas Ege, Dana Rept., No. 31, 1948: 148 pp., (descr., synonymy, zoogeogr.); Haffner, Systematic Zool., *1* (1), 1952: 113-133 (zoogeogr.).

Chauliodus sloani pammelas, Marshall, Aspects Deep Sea Biol., N.Y., 1954: 66 (name).

Probable synonym:

Chauliodus sloanii (partim), Alcock, Descr. Cat. Indian Deep Sea Fishes, Calcutta, 1899: 144 (not seen).

Not *Chauliodus pammelas* Pappenheim, Deutsche Südpolar Exped., *15*, Zool. *7*, 1914: 167 (name, N. Atlantic).

Chauliodus schmidti Ege, 1948

Study material. Thirty-five specimens, 49 to 199 mm standard length from the eastern Atlantic.

Distinctive characters. Chauliodus schmidti is distinguished by the forward position of its dorsal fin, the low number of serial photophores, and the presence of only two larger pigmented light organs in each section of the SM series.

Description. Proportional measurements of the study material expressed as mean percentages of standard length unless noted otherwise, with the range of variation in parentheses.

Body: depth 8.4 (6.3-10.7).

Head: 13.8 (12.2-14.9).

Eye: 3.1 (2.4-4.1); 22.4% of head (18.4%-27.8% of head).

Snout: 3.3 (2.8-3.7); 23.9% of head (20.4%-26.6% of head).

Distance from snout: to origin of dorsal fin 21.4 (19.4-23.4); to origin of anal fin 84.5 (82.8-85.8); to origin of ventral fin 42.9 (39.9-46.0).

Pre-anal length without head: 71 (68-72).

Dorsal fin: rays 6, rarely 5.

Anal fin: rays 10-12.

Pectoral fin: rays 11-13.

Ventral fin: rays 7.

Vertebrae: 52-55 [56].

Branchiostegal rays: 17-19.

Serial photophores: Ventral row: IP 9-11; PV 17-20; VAV 22-25; AC 9-11; Total 60-63. Lateral row: OV 17-20; VAL 21-24; Total 38-42.

Body elongate, slender, compressed, the depth averaging about 1/12 of the standard length. Chin barbel reduced to a stump, at least in adults.

Head 1/8 to 1/7 of standard length, bony ridges present above eyes. Eye round, its diameter averaging a little more than 1/5 head length. Snout generally slightly longer than eye.

Subocular organ present below front of eye, deeply embedded. Postocular organ round, below posterior part of eye.

Mouth large, jaws almost equal to head. Premaxillaries with four teeth, second tooth longest, fourth tooth generally longer than third. Maxillaries with numerous oblique denticles on posterior part of ventral margin, entering gape. Mandibles with five to nine (most often six) larger teeth, and none to two small denticles posteriorly near corner of mouth.

Pectoral fins arising low on body, below posterior part of opercular apparatus, of 11 to 13 rays. Origins of ventral fins close together at midventral line, before middle of standard length, fins with 7 rays. Dorsal with six, rarely five rays, dorsal origin over 5th to 7th OV photophore. Anal origin far behind dorsal, close to caudal, fin with 10 to 12 rays. Caudal fin forked.

Sides of body with five longitudinal rows of scales, the scale areas marked by pigment patterns. Each scale area with one to several small photophores, those of the second row generally with one, sometimes two, of the third and fourth rows with two such organs. Serial photophores located ventral to scale areas of fifth row. SM organs with two larger, pigmented organs in each section, SM formula 1+2+1.

Size. The largest known specimen is something over 200 mm long.

Relationships. C. schmidti is very close to *C. sloani* of the Atlantic, differing from that group in the lower number of serial photophores, and in a tendency for the scale areas of the second row to have only a single small light organ more often than two (see Table II). It would seem that *C. schmidti* has probably developed directly from the Atlantic population of *C. sloani.*

Range. C. schmidti apparently occurs only in the eastern Atlantic, off the coast of Africa, between approximately 10°S and 20°N. Its east-west distribution is as yet unknown. The species has been found at depths as shallow as 25 meters and as great as 3000 meters. The Dana records (Ege, 1948) show that of their 96 specimens, approximately 48 per cent were taken at depths of 50 meters or less, and about 40 per cent came from between 500 and 1500 meters. There seems to be a strong tendency for small individuals, 50 mm or less, to occur above the 500 meter depth, while specimens over 75 mm are most frequently found at depths of 500 meters and more.

Synonyms and references:

Chauliodus sloanei schmidti Ege, Dana Rept., No. 31, 1948: 139 (type descr., type locality "Tropical waters off W. coast of N. Africa; north-eastern South Atlantic, to ca. 8°S."; type specimen Dana Coll. No. St. 4005); Haffner, Systematic Zool., *1* (1), 1952: 113-133 (zoogeogr.).

Chauliodus sloani schmidti Marshall, Aspects of Deep Sea Biology, N.Y., 1954: 66 (name).

Probable synonym:

Chauliodus sloanei (partim) Norman, Discovery Rept., *2*, 1930: 308.

Chauliodus sloani Bloch and Schneider, 1801

Study material. Three hundred and sixty specimens, 25 to 278 mm in standard length, from the Atlantic Ocean, Gulf of Mexico, Mediterranean Sea, eastern, middle and western Pacific Ocean, and the Indian Ocean.

Distinctive characters. Because of the rather wide variation between populations of *C. sloani*, it is difficult to give a succinct summary of its distinctive characters. In general, *C. sloani* may be characterized by a greater number of serial photophores than any species except *C. macouni*, a round postocular organ, and the origin of the dorsal fin over the 5th to 8th OV photophore except in some variants from the Indo-Pacific region. In these, however, if the dorsal origin is over the 9th or 10th OV photophore, the SM organs are 1+3+1 or 1+4+0 in each section, which will separate them from *C. danae* of the Atlantic.

Description. Proportional measurements of the study material given as mean percentages of standard length, except as noted, with the range of variation in parentheses. Data in brackets from other authors.

Body: depth 7.9 (5.6-12.0).

Head: 13.6 (10.5-16.3).

Eye: 3.1 (2.0-4.3); 23.3% of head (19.1%-32.4% of head).

Snout: 3.3 (2.3-4.2); 24.4% of head (17.9%-32.0% of head).

Distance from snout: to origin of dorsal fin 21.4 (17.6-25.8) [27.9]; to origin of anal fin 84.8 (80.8-88.4); to origin of ventral fin 42.1 (38.5-50.0).

Pre-anal length without head: 71 (66-76).

Dorsal fin: rays 6, rarely 5 or 7.

Anal fin: rays 10-13.

Pectoral fin: rays 11-14.
Ventral fin: rays 7, rarely 6 or 8.
Vertebrae: 54-62.
Branchiostegal rays: 15-21.
Serial photophores: Ventral row: IP 8-11; PV 18-22; VAV 24-29; AC 9-13; Total [62] 63-70 [72]. Lateral row: OV 17-22; VAL 23-29; Total 42-49.

Body slender, elongate and compressed, its depth averaging less than 1/12 of the standard length. Chin barbel present in young, slender, tapered, flexible, becoming reduced to a short, triangular stump in adults. Indo-Pacific populations have slightly longer barbels than do Atlantic specimens, and appear to retain the fully developed barbel longer.

Head 1/10 to 1/6 of standard length, bony ridges above eyes. Eye round, its anterior-posterior diameter averaging almost 1/4 of head length, and a little shorter than snout. Snout short, but generally slightly longer than eye. Subocular organ present below anterior part of eye, deeply embedded. Postocular organ round, below posterior part of eye.

Mouth large, jaws almost equal to head. Premaxillaries with four teeth, second longest, fourth tooth usually longer than third. Second tooth, and sometimes third and fourth also, slightly barbed. Maxillary longer than premaxillary, with numerous small, oblique denticles on posterior half of its ventral margin, entering gape. Mandible long and heavy, with five to nine (usually six or seven) large teeth, of which the first is much the longest. Behind these, near corner of mouth, 0 to 10 or more tiny denticles (see Table IV).

Pectoral fins arising below posterior edge of opercular apparatus, low on body, fins of 11 to 14 rays. Origins of ventral fins close together on midventral line, before middle of standard length, fins normally of seven rays, rarely six or eight. Dorsal with six (rarely five or seven) rays, its origin over the 5th to 8th OV photophore in Atlantic and Mediterranean populations, as far posterior as the 10th OV photophore in some Indo-Pacific individuals. Anal origin far behind dorsal, close to caudal, fin of 10 to 13 rays. Caudal fin deeply forked.

Sides of body with five longitudinal rows of scales, each scale area marked off by the underlying pigment pattern in skin. Each scale area with one to several small light organs, those of the second row with one or two organs, those of the third row with two, fourth row with one to three, most often two. In

temperate Atlantic forms, the two organs of the second row are usually unpigmented. In most of the Pacific, Indian and tropical Atlantic populations, the more ventral of the two organs in the second row is usually pigmented. In some Pacific populations, the small unpigmented organ is reduced or absent, and the same is true of many specimens from the Mediterranean Sea. Large serial photophores located ventral to scale areas of fifth row. SM organs vary in number from one population to another. In most Atlantic forms, usually 1+2+1, in Indo-Pacific forms basically 1+3+1 or 1+4+0, with many variations in the number of small anterior and posterior organs.

Size. The largest specimen examined was 278 mm (11 inches) in standard length. Zahl (1953:603) records one from the Mediterranean of 350 mm, which appears to be the largest known.

Relationships. Chauliodus sloani is the most basic form among the modern species of the genus. At least two species, *C. pammelas* in the Indian Ocean, and *C. schmidti* in the Atlantic, appear to have been derived directly from it. *C. macouni* of the North Pacific and *C. danae* from the Atlantic, although undoubtedly derived from a *sloani*-like form, nevertheless show rather more basic differences which suggest that their origins are more remote than those of *C. pammelas* and *C. schmidti.* And *C. barbatus* is obviously the farthest removed, morphologically speaking, from the basic type.

Range. Of world-wide distribution in tropical and temperate seas. In the Indo-Pacific, it is found as far south as approximately 42°S, and north to roughly 32°N. In the Atlantic, the species has been recorded between 36°S and 57°N, with a single record of a specimen washed up on the southeast coast of Iceland at approximately 65°N. It has also been recorded from many stations in the Mediterranean Sea.

Discussion. The description and characterization of *C. sloani* is not made easier by the distressing tendency of this form to split into races which show greater or lesser morphological differentiation, one from another. This has been thoroughly demonstrated by Ege (1948), and is well shown in his illustrations of the condition of the small body photophores in various samples. Although the differences are not as constant as Ege apparently believed, nevertheless, they do represent tendencies within each population. There is, for example, a trend towards pigmentation of both the small light organs in the second scale

row in the tropical forms, while in the populations from temperate areas, these organs tend to be unpigmented. Yet at the same time, greater or lesser numbers of individuals will be found in any of these populations which do not agree with the majority.

Perhaps even more striking is the change in the SM organs with geography. The basic formula in the Indo-Pacific area appears to be 1+3+0, that is, one unpigmented organ at the anterior end of each section, followed by three pigmented organs. But as one progresses eastwards through the Pacific, especially in the Pacific Equatorial Water mass, this formula tends towards 1+3+1 and finally 1+4+0. As far as this particular feature is concerned, it suggests that *C. barbatus,* inhabiting the eastern extreme of the Pacific Equatorial Water, is the end result of whatever forces are at work here, for this species normally has five to seven small pigmented organs in each SM series.

Movement away from the tropics, in a north-south direction, is also reflected in changes in the SM organs. In northern areas of the Pacific, between about 20°N and 32°N, the few specimens available to us showed suggestions of reduction of the pigmentation of the last SM organ. In the temperate Atlantic, both north and south, this condition is much more marked, with perhaps the majority of specimens exhibiting a 1+2+1 condition.

A third characteristic is the length of the barbel, which is shortest in the North Atlantic forms and longest in those from the mid-Pacific. The Indian Ocean specimens are intermediate. Also, the Atlantic *C. sloani* appear to lose their barbels at a smaller size than do the Indian and Pacific ocean members of the species.

All in all, these phenomena are open to at least two interpretations. The first is that each population is more or less isolated by the physico-chemical conditions of the water mass in which it lives, and that the small differences observed from one population to another are the result of reduced genetic interchange between populations as compared to within populations. Without a doubt, this factor is operating but to what extent we cannot tell.

It is also possible to interpret these slight changes in morphology as representing the result of the direct response of the organisms to physical and chemical characteristics of the particular water mass in which they live. We rather lean towards this

interpretation, for we find that *C. sloani, sensu stricto,* occurs in nearly all the water masses of the Indian, Pacific and Atlantic oceans. Water mass boundaries do not appear, on the basis of present information, to be serious barriers for this species.

As far as considering these populations as subspecies is concerned, we have already shown that none of them meet the modern criteria for such a division. There is greater difference, for example, between the North Atlantic and Indian Ocean populations of *C. sloani* than there is between the *"secundus"* and *"dannevigi"* groups, yet no one has yet suggested — nor do we do so now — that the two former groups should be designated as other than populations.

Synonyms and references:

Chauliodus sloani Bloch and Schneider, Systema Ichthylogiae, Berlin, 1801: 430 (type descr.); Cuvier, Regne Animal, Paris, 1836-1849: 232 (descr.); Cuvier and Valenciennes, Histoire Naturelle des Poissons, Paris, Vol. *22,* 1849: 382-389 (descr., synonymy); Canestrini, Fauna d'Italia. Pesci., Milan, 1871-1872: 221 (not seen); Döderlein, Atti Accad. Palermo, (2) *6*, 1878-1879: 56 (name); Jordan and Gilbert, Bull. U.S. Nat. Mus., *16,* 1882: 285 (descr.); Facciola, Nat. sicil., *2,* 1883: 188 (not seen); Jordan, Rep. U.S. Comm. Fish., (1885) 1887: 834 (name); Agassiz, Bull. Mus. Comp. Zool. Harvard, *15*, 1888: fig. 214 (illus.); Vaillant, Exped. Sci. Travailleur et Talisman, 1888: 102 (Morocco); Carus, Prodromus Faun. Med., Stuttgart, vol. *2*, 1889-1893: 570 (name); Goode and Bean, Oceanic Ichthyology, Washington, 1895: 96-97, fig. 115 (descr., illus.); Garman, Mem. Mus. Comp. Zool. Harvard, *24,* 1899: 272-274, Pl. K, fig. 3 (name, comp. with other spp.); Odon de Buen, Bol. Soc. esp. Hist. nat., *2,* 1902: 104-105 (descr.); Jordan and Starks, Bull. U.S. Fish. Comm., *22* (1902) 1904: 579 (name); Regan, Trans. Linn. Soc. Lond., (2) *22*, Zool., 1908: 218 (N. of Peros Banhos Atoll); Weber, Siboga Exped. Fische, 1913: 12-13 (descr.); Weber and de Beaufort, Fishes Indo-Australian Archipelago, Leiden, vol. *2*, 1913: 110, fig. 38 (descr., illus.); Sanzo, Mem. R. Accad. talassogr. ital., *39*, 1914: 1-7, figs. 1, 2 (descr. larvae); Gilbert, Proc. U.S. Nat. Mus., *48,* 1915: 321 (name); Sanzo, R.C. Accad. Lincei, (5a) *27*, 1918: 91-97 (descr. larvae); Gilchrist, Rep. Fish. Mar. Biol. Surv. South Africa, No. 2, Spec. Rep. No. 3, 1921 (1922): 42, 54 (occurrence S. Afr.); Jordan, Evermann and Clark, Rep. U.S. Comm. Fish., (1928) 1930, App. X: 71 (name); Borodin,

Bull. Mus. Comp. Zool. Harvard, *72* (3), 1931: 64 (name, stomach contents); Fowler, Bull. Amer. Mus. Nat. Hist., *70*, 1936: 219-221, 1199 (name, descr.); Bigelow and Schroeder, Fish. Bull., U.S., *74* (vol. 53), 1953: 145-146 (descr.); Tchernavin, Summary of the feeding mechanisms of a deep-sea fish, *Chauliodus sloani*. Brit. Mus. (Nat. Hist.), London, 1953: 101 pp. (anat. head region in relation to feeding); Munro, Marine and Freshwater Fishes of Ceylon, Canberra, 1955: 35 (Gulf of Manar, 500 fath.).

Chauliodus sctinotus Bloch and Schneider, Systema Ichthyologiae, Berlin, 1801: 555, pl. 85 (type descr., illus., type locality Mediterranean Sea); Bonaparte, Iconografia Fauna Italica, III. Pesci., Roma, 1832-1841: fasc. XXX, No. 158, fig. 2 of un-numbered plate (descr., illus.); Catologo Metodico, Napoli, 1846: 35 (name).

Esox stomias Shaw, General Zool., vol. 5 (1), London, 1804: 120, pl. 111 (descr.).

Stomias boa (*Chauliodus schneideri*) Cuvier, Regne Animal Illus., Poissons, Paris, 1817: pl. 97, fig. 3 (illus., not seen).

Stomias schneideri Cuvier, Regne Animal, Paris, 1836-1849: pl. 97, fig. 3 (illus., plate erroneously labelled *Stomias boa*).

Chauliodus schneideri Risso, Histoire Naturelle des Principales Productions de l'Europe Meridionale, vol. III, Paris, 1826: 442, pl. 14, fig. 37 (not seen).

Leptodes sloanii Swainson, Nat. Hist. Classification Fishes, Amphibia, Reptiles, London, 1839: 298 (name).

Chauliodus sloanii (Günther, Cat. Fish. Brit. Mus., vol. *5*, London, 1864: 392 (descr.); Goode, Proc. U.S. Nat. Mus., *3*, 1880: 483 (off So. New England); Vinciguerra, Ann. Mus. Stor. nat. Genova, *22*, 1885: 469-470 (descr.); Günther, Handbuch Ichthyol., Wien, 1886: 453, fig. 324 (not seen); Challenger Rept., Zool. *22*, 1887: 179 (New Guinea, Japan, Atlantic, Bermuda, 565-2575 fath. water); Alcock, Ann. Mag. Nat. Hist., (6) *4*, 1889: 399 (Bay of Bengal, Gulf of Manar); Collett, Bull. Soc. Zool. France, *15*, 1890: 223 (Funchal); Alcock, Ann. Mag. Nat. Hist., (6) *8*, 1891: 127 (occurrence Indian O., ova, pyloric caeca); Descriptive Cat. Indian Deep Sea Fishes, Calcutta, 1899: 355 (not seen); LoBianco, Mitt. Zool. Sta. Neapel, *15*, 1902: 419, 420, 422, 431 (juveniles, Gulf of Naples); Regan, Ann. Mag. Nat. Hist. (9) *11*, 1923: 614 (no. vert.).

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Chauliodus sloanei sloanei Ege, Dana Rept., No. 31, 1948: 1-148 (classification, phylogeny, zoogeogr.); Haffner, Systematic Zool., *1* (3), 1952: 112-133 (zoogeogr.); Koefoed, Rep. Sars N. Atlantic Deep Sea Exped., *4* (2) (5), 1956: 18-19 (N. Atl., misc. discussion).

Chauliodus sloanei dannevigi Ege, Dana Rept., No. 31, 1948: 1-148 (classification, phylogeny, zoogeogr.); Haffner, Systematic Zool., *1* (3), 1952: 112-133 (zoogeogr.).

Chauliodus sloanei secundus Ege, Dana Rept., No. 31, 1948: 1-148 (classification, phylogeny, zoogeogr.), 139 (type descr., type locality N. of Samoa Is., 300 m, type specimen Dana Coll., No. St. 3588 (2)); Haffner, Systematic Zool., *1* (3), 1952: 112-133 (zoogeogr.).

REMARKS ON THE SYNONYMY

Chauliodus barbatus

The most easily distinguished species of the genus, it does not appear to have been given any other name, nor have we found any indication in the literature that it has been reported under a mis-identification. Indeed, it is so different from the other species of the genus that mis-identification hardly seems possible.

Chauliodus danae

Known only from the Atlantic Ocean, this is a well-defined species, with a rather lower number of serial photophores than *C. sloani*. Although Pappenheim (1914: 167) gave no characteristics for his 22 mm specimen of "*C. pammelas*" from the North Atlantic (24°41′N, 32°21′W), it seems probable that the specimen had rather fewer photophores than *C. sloani*, leading him to name it as he did. This, together with the locality of capture, strongly suggests that the specimen was actually *C. danae*.

As Ege (1948: 101) has shown, "*C. danae*" of Phillipps, from Cook Strait, must belong to the "*dannevigi*" population of *C. sloani*.

We have examined the types and paratypes of Barbour's (1942:46) *C. atlantis,* and find that the specimens "too small to be determined with any certainty" belong to *C. danae.*

Chauliodus macouni

We have examined the type specimen of *C. emmelas* in the U.S. National Museum, comparing it directly with the type and other material of *C. macouni* in the same institution. There can be no doubt that the two species are identical. The confusion that has arisen over Jordan and Starks' (1904: 579) statement that the head of *C. emmelas* is 7.5 in length, as compared with "about one sixth" in *C. macouni,* is due entirely to the fact that Jordan and Starks used total length, whereas Bean (1891: 44), in describing *C. macouni,* used standard length. As we have shown, there is no justification for retaining *C. macouni* as a subspecies of *C. sloani.*

Chauliodus pammelas

Ege (1948: 101) points out that some specimens of "*C. sloani*" described by Alcock (1899: 144) have only 61 photophores in the ventral row, which is below the number known for *C. sloani.* It is apparent, then, that these specimens must belong to *C. pammelas.* Pappenheim's specimen of "*C. pammelas*" from the Atlantic has already been discussed under *C. danae.* As with *C. macouni,* we find sufficient divergence between *C. pammelas* and *C. sloani* to indicate that the former cannot be considered as a subspecies of the latter. We have therefore placed *C. s. pammelas* as a full species.

Chauliodus schmidti

Ege (1948: 101) has pointed out that at least some of the material reported as *C. sloani* by Norman (1930: 308) probably belongs to *C. schmidti,* for "the two northernmost catching places, . . . fall within an area off the west coast of Africa, where *Ch. sloanei sloanei* is replaced by the new subspecies *Ch. sloanei schmidti.*"

We have shown above that this form must be regarded as a species closely related to, but separate from *C. sloani.*

Chauliodus sloani

The various ancient names applied to this species are listed in the synonymy, and would seem to present no problems worth noting. A number of authors have followed Swainson (1839) and Günther (1864) in spelling *sloani* with two i's. There is no justification for this, except that it was possibly the fashion in the first half of the 19th century to use this form. Goode and Bean (1879) used the spelling "*sloanei,*" and Jordan and Evermann (1896), evidently justifying their change to this emendation, noted that the species was named for Sir Hans Sloane. However, the spelling of patronymics in those days was a casual matter, and Sir Hans himself was doubtless not entirely certain of the correct spelling. We prefer to maintain Bloch and Schneider's (1801) original orthography of "*sloani.*"

We have examined the type specimen of Garman's *C. dentatus* (Harvard Mus. Comp. Zool., No. 6597), a species long considered distinct because of Garman's (1899) indication that there were 14 AC photophores. Although the specimen is broken in three pieces, nevertheless it is possible to fit the parts together with a fair degree of precision. We counted 10 AC organs, with probably one, possibly two missing from the break in the caudal peduncle, for a maximum AC count of not more than 12. The total count of the ventral row of photophores is either 69 or 70, of the lateral row 48. These counts fall within the upper limits observed for *C. sloani,* and since all other characteristics of the specimen agree well with that species, we have placed *C. dentatus* Garman in the synonymy of *C. sloani.*

Examination of the type and paratype (Harvard Mus. Comp. Zool., Nos. 35621 and 35615) of *C. atlantis* Barbour shows that this species belongs in *C. sloani.* The smaller specimens accompanying the types have already been remarked on.

Chauliodus dannevigi McCulloch falls well within the normal variation of *C. sloani,* according to McCulloch's (1916: 179) description, and is therefore included as a synonym. As Ege (1948) showed, this form represents a more or less discrete group, which Ege considered a subspecies. We find ourselves unable to agree with this interpretation, considering *dannevigi* to represent a population no more divergent than several others, e.g. that from the Sulu Sea. The same is true of the form described by Ege as *C. sloanei secundus,* as shown in the early pages of the present paper.

SUMMARY

Specimens of all known species of *Chauliodus* have been examined, including the types of *C. barbatus, C. macouni, C. emmelas, C. dentatus,* and *C. atlantis.* As a result, only six species of *Chauliodus, C. barbatus, C. danae, C. macouni, C. pammelas, C. schmidti* and *C. sloani,* are maintained. All other species have been found to be synonyms. The several subspecies proposed by Ege have been shown to be either fully recognizable as species or else to be no more distinct than more or less discrete populations of *C. sloani.*

LIST OF SPECIMENS[1]

Chauliodus barbatus. Harvard Mus. Comp. Zool., Nos. 28489, 28490 (types); U.S. Nat. Mus., Nos. 148239, 151225; Zool. Mus. Univ. Copenhagen, "Galathea" Coll., Nos. 12, 13, 14, 15; Stanford Univ. Zool. Mus., No. 25314; Scripps Inst. Oceanogr., Nos. 52-363 (2), 52-390, 52-404, 55-244, 55-246, 55-258 (3), 55-265.

Chauliodus danae. Bingham Oceanogr. Coll., Nos. 2928 (6), 2929 (3), 2931, 2932, 2933, 2934 (2), 2935, 2936 (2), 2937, 2938 (5), 2939 (6), 2940 (4), 2941 (2), 3211 (3), 3766, uncatalogued (8); Harvard Mus. Comp. Zool., Nos. 32277 (2), 34956 (9), 34983 (2), 35165, 35620 (3); U.S. Nat. Mus., Nos. 89914, 100336, 100565, 117872, 117874 (2).

Chauliodus macouni. U.S. Nat. Mus., Nos. 45372 (type), 51464 (type of *C. emmelas*), 53946, 77462, 125340, 132131 (2), 150088, 150089, 150090; U.S. Fish Wildl. Serv. Lab., Honolulu, Nos. 1778 (3), 1780 (3), 1781, 1783; Stanford Univ. Zool. Mus., Nos. 2000, 5259, 24950 (7); Scripps Inst. Oceanogr., Nos. 51-373 (4), 53-332 (3); Univ. Wash. Coll. Fish., uncatalogued (2); Univ. Wash. Dept. Oceanogr., uncatalogued (57).

Chauliodus pammelas. British Museum (Natural History), Nos. 1939.5.24.410, 1939.5.24.411, 1939.5.24.413, 1939.5.24.414, 1939.5.24.415, 1939.5.24.416, 1939.5.24.417.

Chauliodus schmidti. Marinbiol. Lab. Charlottenlund, Dana Coll., Nos. 3999 I, 4000 VI, 4000 X, 4003 V, 4003 VII (2), 4004 I (3), 4005 I, 4005 III, 4005 V, 4005 VII (7), 4006 I (8), 4006 II, 4007 I (3), 4007 VI (3), 4007 IX.

Chauliodus sloani. Bingham Oceanogr. Coll., Nos. 415 (2), 2915, 2916 (2), 2917 (2), 2918 (5), 2919, 2922 (4), 2924, 2925,

[1] Numbers in parentheses indicate number of specimens if more than one.

uncatalogued (4); Harvard Mus. Comp. Zool., Nos. 3903 (13), 26405 (2), 31607 (4), 31608 (6), 31609, 31610, 32274, 32275, 32276, 34949, 34952 (5), 34954 (2), 34978, 34982 (2), 35095, 35099, 36598, 39433 (5), 39726; Marinbiol. Lab., Charlottenlund, Dana Coll., Nos. 3676 II (3), 3678 IV (4), 3678 VI, 3680 VI (7), 3680 VIII (4), 3681 I (4), 3682 I, 3683 I (3), 3683 IV (6), 3683 VI (5), 3683 VII, 3684 VI (2), 3685 I (21), 3685 IX (3), 3686 VIII (4), 3735 I (6), 3735 II (6), 3736 I (8), 3736 III (5), 3736 V (9), 3736 VI (2), 3737 I (18), 3737 II, 3738 I (8), 3738 II, 3738 III (2), 3739 I (4), 3739 VI, 3739 VII, 3739 IX (2), 3740 I (4), 3740 II (2), 3925 II (3), 3933 III. 3949 I (2), 3953 I (2); as *C. sloanei dannevigi* 3587 IX, 3601 I (2), 3613 VI, 3624 I, 3625 I, 3627 VI, 3630 II, 3631 II (2), 3631 III, 3639 I, 3640 I, 3640 III, 3651 I (3), 3651 VI, 3653 I, 3654 I, 3655 V (4), 3656 I, 3656 III, 3663 I, 3663 VIII (3), 3664 IV (3); as *C. sloanei secundus* 3584 I, 3716 II (2), 3766 VIII (5), 3766 XIII, 3768 V, 3809 II (23), 3830 V (2), 3881 I (4), 3881 II (5), 3934 I+VI+XI (3), 3934 II+VII+XII (5), 3934 III+VIII+XIII (4), 3951 I, 3969 IV; Scripps Inst. Oceanogr., No. 52-404 (3); U.S. Fish Wildl. Serv. Lab., Honolulu, 1782, 1917, 1918, 1919 (2), 1922, 1923, 1924 (2), 1926 (2), 2336, 2338, 2339 (2), 2340, 2341; U.S. Nat. Mus., Nos. 39218, 44402, 89915, 92246 (2), 117873, 131598, 143060, 158832, 159889, 163490 (2), 185590, 185591 (6), 185592 (2), 185593, 185594; Univ. Miami Mar. Lab., Nos. 590, 716, 1623, 1632, 2004.

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A CONTRIBUTION TO THE BIOLOGY OF THE GIGANTURIDAE, WITH DESCRIPTION OF A NEW GENUS AND SPECIES

By Vladimir Walters
American Museum of Natural History

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
October, 1961

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No. 10— *A Contribution to the Biology of the Giganturidae, with Description of a New Genus and Species*[1]

By Vladimir Walters

INTRODUCTION

The morphology of the giganturid fishes is imperfectly known. Brauer (1908) described the structure of the eye of *Gigantura indica,* and Bierbaum (1914) worked out the structure of the labyrinth of *G. chuni.* The osteology of *G. vorax* was studied by Regan (1925). While preparing an account of the Giganturidae for a forthcoming volume of "Fishes of the Western North Atlantic" I found it necessary to investigate the anatomy of the specimens, since many of their external features had been destroyed.

William C. Schroeder and Mrs. Myvanwy Dick of the Museum of Comparative Zoology, and James E. Morrow of the Bingham Oceanographic Laboratory generously loaned their specimens of *Gigantura vorax.* Through the kindness of Carl L. Hubbs and Alfred Ebeling of the Scripps Institution of Oceanography, two specimens of unidentified Pacific giganturids were borrowed for comparison with *G. vorax.* I am grateful to N. B. Marshall of the British Museum (Natural History) who examined the types of *G. vorax* Regan and *G. gracilis* Regan both in the British Museum and in the Dana collections in Copenhagen. An expression of appreciation is due Giles W. Mead of the Museum of Comparative Zoology who provided his manuscript revisions of five families of iniomous fishes, and who forwarded material belonging to various synodontoid genera. James E. Böhlke of the Academy of Natural Sciences at Philadelphia, Daniel M. Cohen of the U. S. Fish and Wildlife Service, Giles W. Mead, and William A. Gosline of the University of Hawaii critically read this manuscript. The sections dealing with the nervous system, sense organs and sensory cues were read by Lester R. Aronson of this Museum, and his suggestions and criticisms are appreciated. Samuel B. McDowell, Jr. aided in some of the dissections and interpretations of structure,

[1] A more general account of the Giganturoidea will appear in Part 4, "Fishes of the Western North Atlantic." Parts of these giganturid studies have been supported by funds granted by the National Science Foundation (N.S.F. Grant 7123) to the Sears Foundation for Marine Research, Yale University.

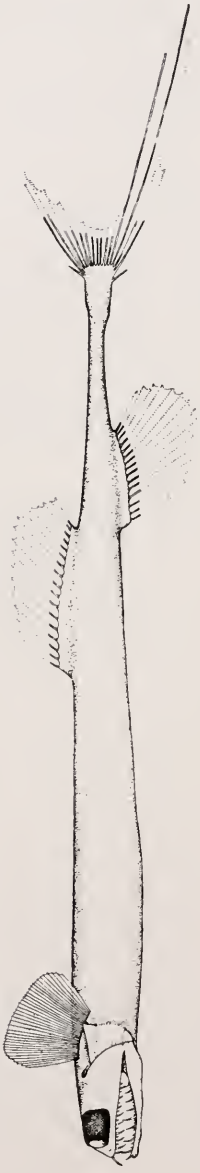

Figure 1. *Bathyleptus lisae*, reconstructed from holotype.

including examinations of members of other groups which formed the background for the phylogenetic assessment of the Giganturidae. The drawings were made by Nina Williams and Samuel B. McDowell, Jr.

Some of my observations (on other species) are at variance with Regan's (1925) diagnosis of *Gigantura* and with his osteological account of *G. vorax*. For instance, none of my specimens have vomerine teeth while *G. vorax* is said to have two vomerine teeth, one behind the other; in *G. vorax* the scapula bears some

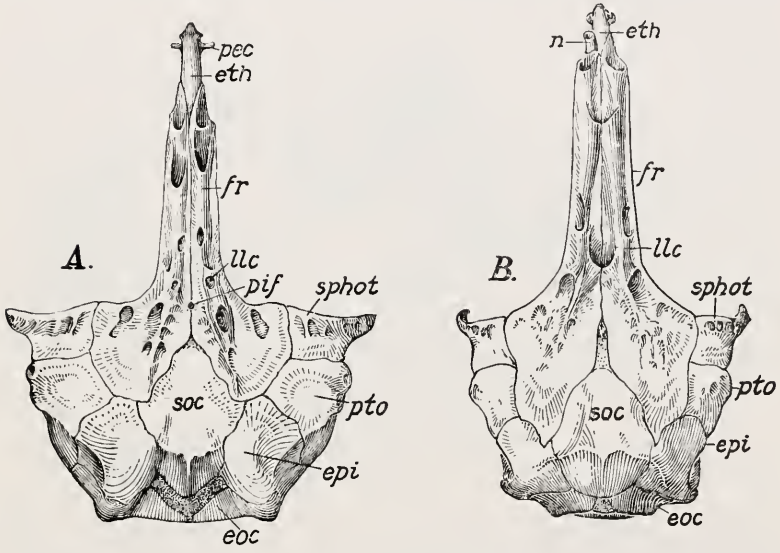

Figure 2. Skull in dorsal aspect. A. *Bathyleptus lisae,* holotype. B. *Gigantura vorax,* American Museum of Natural History 20393. See legend of Figure 3 for key to abbreviations.

of the fin-rays, the cleithrum extends the full length of the girdle and there is no posterior coracoid process, while in my material the scapula does not support any fin-rays, there is no cleithrum, and the coracoid bears a posterior process. Marshall's re-examination of Regan's material (both *gracilis* and *vorax*) failed to disclose vomerine teeth, and the pectoral girdle, which Regan illustrated, has either been discarded or lost. Marshall also believes that the neurocranium of the type of *G. vorax* more closely resembles the figures given below than it resembles Regan's figures.

MORPHOLOGY

(Figures 2 to 7)

Visceral Arches. All that remains of the hyoid arch in *Gigantura* and *Bathyleptus* are the hyomandibular and the quadrate; the ventral elements of this arch and the branchiostegal rays are absent. There do not seem to be any cartilages either supporting or associated with the gills. In both genera the first gill slit is the longest and lenticular, the second is shorter and elliptical,

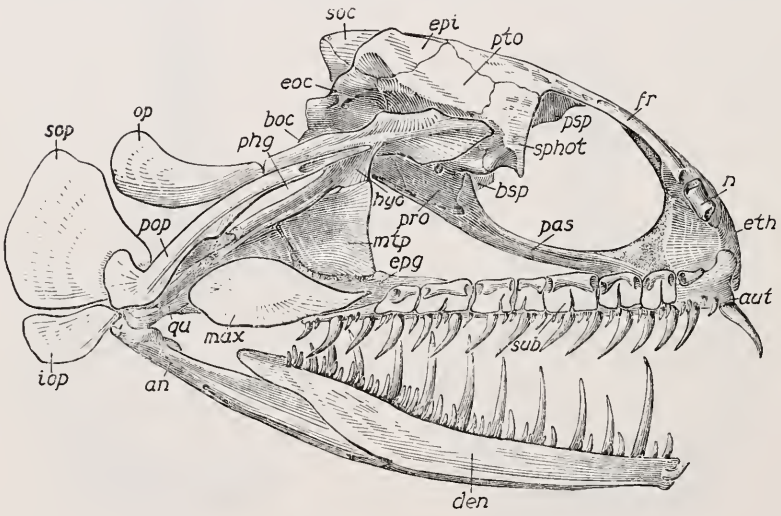

Figure 3. Skull of *Gigantura vorax* in lateral aspect, composite. Abbreviations: *an,* angular; *aut,* autopalatine; *boc,* basiocciptal; *bsp,* basisphenoid; *den,* dentary; *eoc,* exoccipital; *epg,* ectopterygoid; *epi,* epiotic; *eth,* mesethmoid; *fr,* frontal; *hyo,* hyomandibular; *iop,* interopercular; *llc,* supraorbital lateralis canal; *max,* maxilla; *mtp,* metapterygoid; *n,* nasal; *op,* opercular; *pas,* parasphenoid; *pcc,* preethmoid cornu; *phg,* preopercular-hyomandibular gap; *pif,* pineal foramen; *pop,* preopercular; *pro,* prootic; *psp,* pterosphenoid (alisphenoid); *pto,* pterotic; *qu,* quadrate; *soc,* supraoccipital; *sop,* subopercular; *sphot,* sphenotic; *sub,* suborbital (?).

the third is shorter and D-shaped, the fourth is very small and circular, and there is no slit behind the hemibranch. In both genera the anterior set of pharyngeal teeth is in the roof of the pharynx behind the last gill slit and anterior to the suspensoria, while the posterior set is in the roof of the esophagus

medial to the kidneys. The posterior pharyngeal arch is the most complete of the post-mandibular arches, consisting of a backwardly directed pharyngobranchial cartilage (toothed), epibranchial and ceratobranchial cartilages in line and sloping downward and backward, and a forwardly-directed hypobranchial cartilage. There is no basibranchial cartilage. The appearance of this arch is Z-shaped. The anterior set of pharyngeal teeth connects with the posterior set, and presumably represents the pharyngobranchial part of the last gill arch.[1]

Viscera. In both genera the kidneys are in the body wall between the epaxial and hypaxial musculature close behind the pectoral girdle; they are triangular and pale-colored with discrete black spots. The anterior location of the kidneys indicates that they may be pronephric, though they are not near the heart. The excretory ducts follow retroperitoneal paths lateral to the mesogasters and enter the urinary bladder beneath the dorsal fin; the bladder discharges to the outside through a urinogenital papilla. The ovaries are hollow sacs, fused posteriorly, and in *Gigantura* they either discharge into the urinary duct below the bladder or open to the outside so close to the bladder that separate openings (if these exist) could not be found in the material examined. The gross anatomy of the male urinogenital system is unknown. In *Bathyleptus* the gonads are missing from both specimens and the excretory duct cannot be traced much beyond the rear of the stomach.

In both genera the cartilages of the pharyngeal arch embrace the roof and sides of the esophagus; a short muscle passes from the lower end of the ceratobranchial and ends in a band of muscle applied to the ventral face of the esophagus. The cartilages have several bands of muscle between themselves and the two sets of pharyngeal teeth. The posterior pharyngeals have a set of retractor muscles which originate above the pyloric valve in *Bathyleptus,* and above the posterior half of the stomach in *Gigantura;* these retractors pass forward between the two sheets of mesogaster and are inserted on the entire upper surface of the posterior pharyngeals. In both genera the stomach is a thick-walled blind pouch; when not distended with food

[1] If we follow the system of E. Jarvik (1954 On the visceral skeleton of *Eusthenopteron* with a discussion of the parasphenoid and the palatoquadrate of fishes. Kgl. Svensk. Veten. Hand. (4) *5* (1): 1-104.) the anterior pharyngeal set represents the infrapharyngobranchial and the posterior set the suprapharyngobranchial elements of the same gill arch.

it is more than half the length of the body cavity and terminates shortly in advance of the dorsal fin (in both specimens of *Bathyleptus* the posterior end of the stomach is missing). The inner lining, about one-quarter to one-third the total thickness of the wall, is white and thrown into deep longitudinal folds.

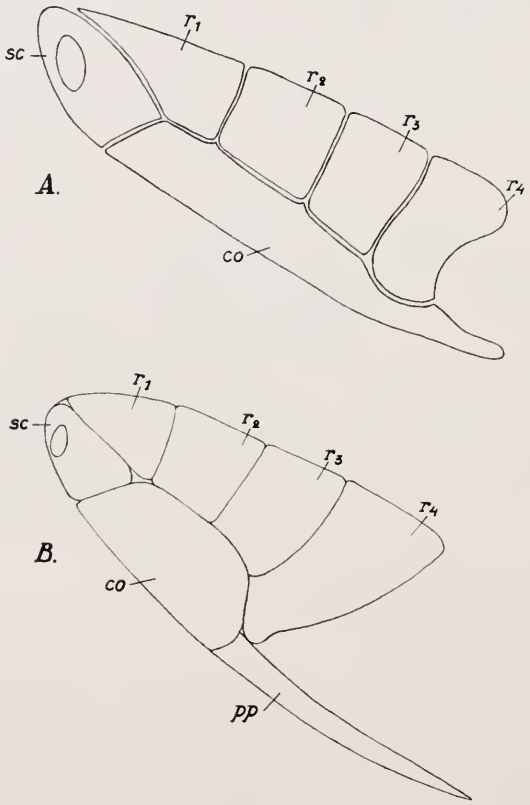

Figure 4. Left pectoral girdle in lateral aspect. A. *Bathyleptus lisae*, paratype. B. *Gigantura vorax*. Bingham Oceanographic Collection 3228. Abbreviations: *co*, coracoid; r_1-r_4, radials; *pp*, postcoracoid process; *sc*, scapula.

This is surrounded by a thick layer of intensely black material. External to the pigmented layer is the serosa. The stomach hangs in the body cavity, suspended on each side by the mesogaster, which is muscular near the esophagus. The intestine, which is colorless, leaves the pylorus near the midline, makes a few small curves along which it receives ducts from the liver and

pancreas, ascends to the dorsal part of the body cavity, passes caudad to the right of the mesogaster, turns ventrad between the unfused lobes of the ovary, and terminates in an anal papilla immediately in front of the urinogenital papilla. The course of the intestine could not be followed beyond the torn end of the stomach in *Bathyleptus*. There is one small pyloric caecum. The astonishingly small orange-colored liver consists of three lobes; in *Bathyleptus* the left-hand pair are joined while in *Gigantura* the right-hand pair are joined. In *Bathyleptus* the liver lobes are horizontal; in *Gigantura* they are vertical. In *Bathyleptus* the lobes are entire but in *Gigantura* the right pair are subdivided into lobules.

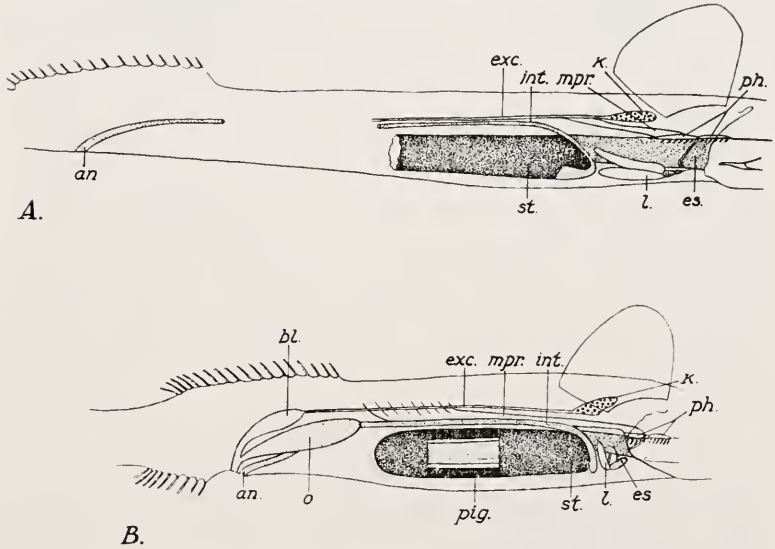

Figure 5. Visceral relations. A. *Bathyleptus lisae*, holotype. B. *Gigantura vorax*, composite drawing. Abbreviations: *an*, anus; *bl*, urinary bladder; *es*, esophagus; *exc*, excretory duct; *int*, intestine; *k*, kidney; *l*, lobe of liver; *mpr*, pharyngeal retractor muscle; *o*, ovary; *ph*, anterior and posterior sets of pharyngeal teeth; *pig*, deeply pigmented layer in stomach wall; *st*. stomach.

Circulatory System. In *Gigantura* the pericardium is embraced by the liver, the ducts of Cuvier enter the short sinus venosus beneath the middle of the ventricle, the truncus arteriosus is robust and conical, and three pairs of aortic arches arise almost simultaneously from its anterior end. In *Bathyleptus* the

pericardium is anterior to the liver, the ducts of Cuvier enter the long sinus venosus posterior to the ventricle, the truncus arteriosus is small and bulbous, and three pairs of aortic arches emerge from the short ventral aorta. In both genera the aortic arches pass forward between the pharyngeal visceral arches before turning laterally and dorsally toward the gills. In both genera the thyroid gland is anterior to the ventral aorta, and apparently has no connection with the esophagus.

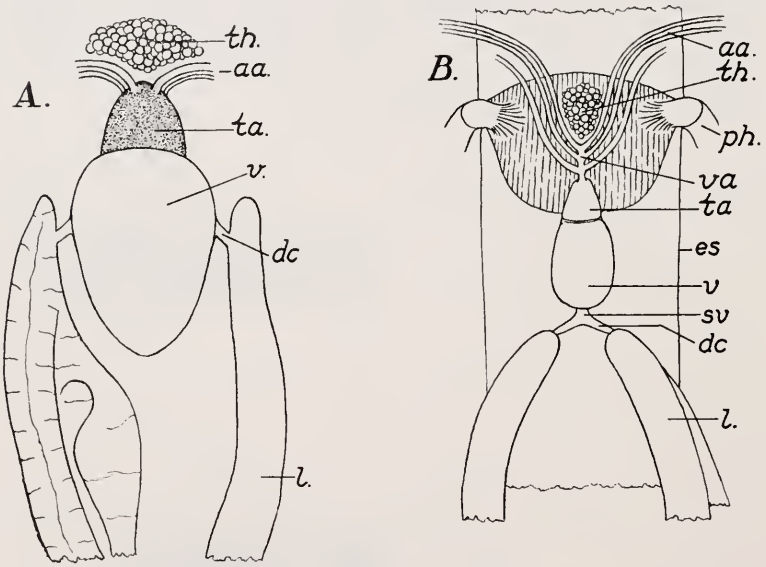

Figure 6. Heart and nearby structures in ventral aspect. A. *Gigantura vorax,* Bingham Oceanographic Collection 3228. B. *Bathyleptus lisae,* holotype. Abbreviations: *aa,* aortic arches; *dc,* duct of Cuvier; *es,* esophagus; *l,* lobe of liver; *ph,* pharyngeal arch; *sv,* sinus venosus; *ta,* truncus arteriosus; *th,* thyroid gland; *v,* ventricle; *va,* ventral aorta.

Brain, Cranial Nerves and Sense Organs. The brain of *G. vorax* has been examined. In the paratype of *B. lisae* the head and brain are crushed, but the outline of the brain is visible through the roof of the holotype skull (cf. Brauer, 1908, table 42, fig. 18 for a figure of such a view of the brain of *B. indicus*). From what can be seen, there do not appear to be any major differences between the brains of the two genera. The forebrain is very small. The enormous optic lobes are followed by the enlarged cerebellum which does not override the optic lobes.

The walls of the medulla oblongata are thickened but there are no enlarged sensory lobes. The stoutest cranial nerves are the auditory (VIII), facial (VII), trigeminal (V), and optic (II); the olfactory (I), oculomotor (III), trochlear (IV), and abducens (VI) are thread-like; the glossopharyngeal (IX) and vagus (X) are intermediate in stoutness. The pineal body is large and applied to the inner surface of the frontals near the supraoccipital; *B. lisae* has a foramen above the pineal, but in *G. vorax* the frontals are separated by a cartilaginous wedge over the pineal. The pineal stalk is remarkably long and robust; at the rear of the stalk is a pair of macroscopic habenular bodies (microscopic in most teleosts). The hypophysis has a remarkably long and slender stalk.

The labyrinth of *Gigantura chuni* was studied by Bierbaum (1914); the sacculus is smaller than the utriculus. In a specimen in the American Museum of Natural History (No. 20393) the plane of the horizontal semicircular canal parallels the longitudinal axis of the head and body. The eye of *B. inducus* was described in detail by Brauer (1908); my material of *B. lisae* and *G. vorax* has not been studied in this regard. The olfactory capsule is almost microscopic and the slender olfactory nerve passes through the orbit dorsal and medial to the oblique muscles (in both genera). The lateral line system is fairly well developed on the head although difficult to trace in entirety owing to loss of skin; the infraorbital canal is particularly well developed in *Gigantura*, and is contained in flexible lightly-ossified

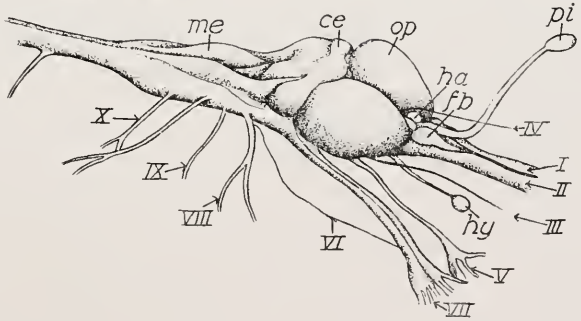

Figure 7. Brain and cranial nerves of *Gigantura vorax*, American Museum of Natural History 20393. Abbreviations: *I*, olfactory n.; *II*, optic n.; *III*, oculomotor n.; *IV*, trochlear n.; *V*, trigeminal n.; *VI*, abducens n.; *VII*, facial n.: *VIII*, auditory n.: *IX*, glossopharyngeal n.; *X*, vagus n.; *ce*, cerebellum; *fb*, forebrain; *ha*, habenular body; *hy*, hypophysis; *me*, medulla oblongata; *op*, optic lobe; *pi*, pineal body.

plates (? suborbitals) fringing the border of the mouth like a transparent curtain. The vagus nerve was followed along the trunk but a lateral line branch was not found; there may not be a trunk lateral line in these fishes.

BIOLOGY OF THE GIGANTURIDAE

General Considerations. The giganturids are mesopelagic predators. All of the energy in the mesopelagic fauna is derived from the photosynthetic processes of algae in the surface layers of the sea; its downward flow is mediated principally through the activities of diurnal vertical migrators which feed in the upper levels and are in turn fed upon in the lower levels. Lesser amounts of energy filter downward in the form of sinking detritus. The deeper the level at which feeding takes place, or in other words the greater the number of steps removed from the primary surface production, the smaller is the amount of food energy that is available for the biomass feeding at that particular level.[1] The size and composition of the population at any feeding level in the ocean is determined by the quantities of food energy entering and of heat leaving that population per time unit; a state of dynamic equilibrium exists and if the flow rate of energy out of the population can be reduced the result would be an increase in the biomass. The flow of energy to the physical surroundings (hence its escape from the biological system) can be attenuated by reducing the rate of metabolism. It is postulated that evolution in the mesopelagic and bathypelagic biomasses has tended toward a reduction in the rate of loss of heat energy to the physical surroundings through a reduction in the metabolic rate.

The giganturids may have achieved metabolic economies in several ways. By reducing the ossification of the skeleton, and by retaining cartilage, the density of the fish is lowered. A further reduction in density is achieved by flooding the subdermal areas with a mesenchymal jelly. Having achieved a density close to that of the surrounding water, the giganturid has no need for a swimbladder and this structure is absent.

[1] Although a mole of glucose contains about 675,000 calories, only 40 moles of pyrophosphate with an energy content of about 400,000 calories are produced when a mole of glucose is biologically oxidized to carbon dioxide and water. In other words, some 275,000 calories per mole of glucose are lost from the biomass at each link in the food chain.

Absence of the swimbladder eliminates the energy expenditure necessary (in other fishes) for the maintenance of a gas bubble at mesopelagial and bathypelagial pressures (see also Jones, 1957, p. 317).

On a wet weight basis, bathypelagic fishes which lack a swimbladder (*Gonostoma elongatum, Xenodermichthys copei*) have 26 to 44 per cent of the protein content of shallow water species with swimbladders (*Ctenolabrus rupestris, Labrus bergylta*) (calculated from Denton and Marshall, 1958: table 1). This suggests that the bathypelagic fishes have a metabolic level approximately one-third that of the coastal forms. The bathypelagic species were found to have dry weights 35 to 48 per cent that of *Ctenolabrus rupestris* (recalculated by author); therefore, the bathypelagic forms have about two and one-half times the water content of the coastal form, and, as Denton and Marshall point out, the higher water content reduces the density of the bathypelagic species. The ash of *Ctenolabrus* weighs about 1.8 to 2.4 times as much as the ash of *Xenodermichthys,* which reflects the heavier and more extensive ossification of the coastal species. Thus, Denton and Marshall's determinations are in accord with my deductions concerning the Giganturidae.

Parr (1937) suggested that the animals of the deep sea constitute a "rachitic fauna" since they are not exposed to sunlight and live with little or no vitamin D; this was offered to explain the feeble ossification of deep-sea fishes. Marshall (1955: 324-325) pointed out that abyssal benthic fishes are well ossified, while some bathypelagic forms which are poorly ossified live at levels not very far removed from the layers where vitamin D is produced. The preceding paragraphs offer an alternative explanation for the reduced ossification of some mesopelagic and bathypelagic fishes; it is likely that there are sufficient amounts of vitamin D at all levels in the ocean, maintained through the activities of vertical migrators.

It is my opinion that neoteny, indications of which are widespread in many deep-sea groups, has been one of the major avenues of evolution in the energy-poor deep-sea environment. Neoteny eliminates part or all of the mainly catabolic phase of life history, which is metabolically the most wasteful portion, and by eliminating the morphogenesis of "adult" structures neoteny may conserve additional amounts of energy for the biomass.

Sensory Cues. The enormous eyes, stout optic nerves, and large optic lobes suggest that vision is important in the giganturid life history. In contrast olfaction is of minor importance; witness the minute olfactory capsule, thread-like olfactory nerves and the minute forebrain. The other chemical sense, taste, is evidently poorly developed since there are no strong sensory enlargements in the medulla. The large cerebellum, stout auditory nerve and small saeculus are indicative of a poor auditory sense and a highly-developed sense of balance. The large trigeminal and facial nerves are partly associated with the cephalic lateral-line system which is best developed along the border of the upper jaw and apparently is of importance in feeding. The enlarged pineal body, its robust stalk, and the large habenular bodies may be associated with control of the response to variations in ambient light intensity. Rasquin (1958) discussed in detail the teleost pineal body and cited literature pertaining to the role of the pineal in governing the response to light.

Denton and Warren (1957) calculated that teleosts should be able to see daylight down to a depth of 1150 meters. This is about the lower limit at which *Gigantura chuni* was collected (660 fathoms); *Bathyleptus lisae* was taken in nets trawled at 1790 and 2140 fathoms but the actual depth of capture may have been shallower. Weale (1955) noted that since in man the threshold for light perception is 10 per cent lower for binocular vision than for monocular vision, binocular vision in deep-sea teleosts may double the visual response at illumination levels near the threshold for monocular vision. Thus giganturids, which evidently possess binocular vision, should be able to see their prey against an illuminated background throughout their vertical range. They may hunt visually at light intensity levels which are too low to enable the prey to see them well. They may follow the deep scattering layers and prey upon the luminous members of these layers, their silvery coloration allowing them to blend inconspicuously with the illuminated background.

Swimming. The small number of vertebrae (about 30) indicates that when a giganturid swims by producing lateral undulatory movements of its body it employs the carangiform rather than the anguilliform type of locomotion. The slight side-to-side movement of the head during carangiform swimming would aid in the search for food by broadening the horizontal sweep of the visual field.

The plane of the horizontal semicircular canal being parallel with the longitudinal axis of the body and the pineal body being exposed through the roof of the skull indicate that giganturids position themselves normal to the pull of gravity and normal to the path of daylight, thus probably swimming horizontally.

The long lower caudal fin lobe may stabilize forward movement in the yawing plane by lengthening the postanal part of the fish so that the dorsal and anal fins lie in the first quarter of the total length and pull rather than push the fish through the water. The asymmetry of the caudal fin would pitch the snout downward if the fin serves as a passive stabilizer and upward if it is used to propel the fish. That the long lower caudal lobe serves a passive, stabilizing role is indicated by the positions of the pectoral fin bases which are somewhat higher in front and would provide lift at the anterior end as the fish moves forward, thereby offsetting the downpitch of the asymmetrical caudal fin. The main propulsive force in swimming is apparently derived from the muscular-based dorsal, anal and pectoral fins.

Feeding. The gape of the mouth converges with the line of sight. When prey is seen, the giganturid may slowly drift in along its line of sight. When close enough so that a visual image is in proper register on the retinas of both eyes, the fish may pounce forward and seize its prey. Since the giganturid cannot see what it swallows, the last-second location of the potential food would be assumed by the infraorbital lateral line canals.

The sharp, recurved, depressible teeth indicate that once prey has been grasped there is no escape; and once it has been seized, it must be swallowed. The prey is manipulated to the rear of the mouth, perhaps through lurching and biting movements of the giganturid. Eventually the anterior set of pharyngeal teeth is able to grasp it, and their stoking actions start the food on its way down the esophagus. The posterior set of pharyngeal teeth does most of the work in packing food into the stomach, by rhythmic contractions of the powerful retractor muscles. The pharyngeal retractors are antagonized by the trunk musculature, which keeps the head and anterior trunk rigid during swallowing (although in some preserved specimens the pharyngeal retractors are contracted and the neck is distorted). The pharyngeal visceral arch is used to maintain a firm grip on the food while it is in the esophagus. In this way it would quiet the struggles of the prey and thus prevent damage to the giganturid's heart and aortic arches, which are otherwise

unprotected. The mesogaster, which is muscular anteriorly, may further aid in quieting the struggles of the prey.

Regan (1925) found a *Chauliodus* 140 mm. long in the stomach of a *Gigantura vorax* 80 mm. long. A *Gonostoma* 86-mm. long was found in the stomach of a 77-mm. *Gigantura vorax* (MCZ 35605). In both cases the tail and head of the food animal were intact while its mid-body which, to judge by its position in the stomach was swallowed first, was well-digested. These observations indicate that the giganturid requires a fairly long time to swallow a large victim. Since a 65-mm. *Gigantura vorax* (MCZ 40706) contained an intact 36-mm. *Cyclothone* sp. in its stomach, we surmise that small prey can be swallowed relatively quickly. In addition to respiratory problems which are discussed below, the giganturid is vulnerable to attack from other predators while it is engaged in swallowing luminous prey. Perhaps the giganturid packs as much as possible of the victim into its stomach as quickly as possible and then closes its mouth over the remainder which fits into the distensible, black-lined throat.

The thick deeply-pigmented layers of the distensible stomach would conceal whatever light may be emitted by the victim while it is being digested. When the food passes to the colorless intestine it is presumably no longer luminescent.

The body cavity accommodates the enormous distention of the stomach while a meal is being digested. The viscera are crowded to the anterior and posterior ends of the body cavity, out of the way of the stomach. The intestine runs dorsal to the stomach. Without such an arrangement of its organs, the giganturid would suffer intestinal strangulation and other discomforts with each hearty meal.

Respiration. The small sizes of the second, third and fourth gill slits and the absence of the gill flap from the upper end of the gill cover indicate that giganturids do not respire in normal teleostean fashion. Regan (1925) suggested that the pectoral fins fan water into the gill chamber, but this is unlikely since the gill flap would interfere while the portion which is not covered by the gill flap is anterior to the pectoral fin. Hence the giganturid probably respires by moving its suspensoria. When the suspensoria expand, some water enters the gill chamber from the pharynx via the first gill slit, when the fish is not feeding. Water can also enter the gill chamber from the outside anterior to the pectoral fin and gill flap. During inspiration the flexible flap would be pressed against the body wall. Since the pectoral

fin base projects forward in the gill chamber over two sets of gills, movements of the fin muscles could aid in mixing the water in the chamber and bathing the gills. During expiration the gill flap lifts away from the body wall and water leaves along the entire length of the gill cover. The beating of the pectoral fins wafts the water downward, backward, and away from the gill chamber. While engaged in swallowing, the giganturid would not obtain any oxygenated water via the pharynx; all would come from the outside.

SYSTEMATIC POSITION OF THE GIGANTURIDAE

Brauer (1901, 1906) compared *Gigantura* (and *Bathyleptus*) with the original description and figure of *Stylephorus chordatus*, later shown to be an allotriognath. Regan's (1925) derivation of the Giganturidae from the Synodontidae is discussed below. Berg (1940) named the order Giganturiformes, following Regan in part. Tchernavin (1947a) corrected Berg's diagnosis of the order and compared *Gigantura* with the Lyomeri without success because the anatomy of *Gigantura* was not well enough known. Fowler (1936, 1958) combined *Gigantura* and *Stylephorus* in one suborder; I have examined *Stylephorus chordatus* and cannot agree with Fowler. Bertin and Arambourg (1958) placed the Giganturiformes between the Synbranchiformes (*sic*) and Saccopharyngiformes (= Lyomeri) without presenting any new information.

Adult giganturids possess certain features which are associated with early developmental stages in other teleost groups: the kidney is anteriorly placed; the fin-rays are not segmented; copious amounts of mesenchymal jelly underlie the skin; scales are absent; the cartilaginous endocranium persists; a vagal portion of the lateralis system seems to be absent; bones and cartilages are absent from the gill supports; there are no gill rakers; the dermal elements of the pectoral arch are missing; and the pectoral girdle has a posteoraeoid process; the ventral elements of the hyoid arch, including branchiostegal rays, are missing; various dermal bones of the skull are missing such as parietals, opisthotics, and premaxillae. Thus, the Giganturidae show evidence of having become neotenic or larvalized.

Gosline (1959) thought it strange that neoteny is rare in teleosts. Actually it is not. Extreme cases of nearly complete larvalization, such as in *Schindleria*, are seldom found, but there is a broad transition zone from this one extreme to the

other in which the adult differs considerably from the immature stages (e.g., eels). The Giganturidae belong in this transition zone. The manifestation of neoteny, whether slight or considerable, implies that relationships of the group cannot be assessed unless the comparisons are confined to similarities or dissimilarities in ontogenetically equivalent structures.

If those features which appear to be neotenic were momentarily left out of consideration, the Giganturidae may be looked on as mesopelagic synodontoids. ("Synodontoid" = belonging or allied to the series of families Synodontidae-Bathysauridae-Harpadontidae.) In fact, Regan (1925) derived the giganturids from the synodontids, and there is a superficial resemblance due mainly to the backward extension of the jaws in both groups; the suspensoria have become backwardly-directed, evenly-curved arches and their caudad swing has rotated the bones of the gill cover so that the subopercular excludes the opercular from the hind margin of the gill flap, and the pharyngeal teeth now lie between the suspensoria. In the Harpadontidae (*Harpadon nehereus*, *H. microchir*), the pectoral girdle approaches the giganturid condition in that the posttemporal connects to the skull by muscle instead of a bone-to-bone contact, but the harpadontid girdle is still well developed and has all elements. Regan's assessment of the relationships of the Giganturidae might have been different had he noted the weakly-ossified lamina which lies buried in the cheek above and behind the "premaxilla"; apparently, this lamina was lost during the preparation of Regan's material.

The feature which distinguishes the iniomous fishes from less advanced teleosts is that the maxillae are excluded from the gape by the premaxillae, which alone border the upper jaw. The dentigerous bone in the upper jaw of the Giganturidae was identified by Regan (1925) as the premaxilla, but by Berg (1940) as the maxilla. Actually this bone might conceivably be any one of the following: 1) premaxilla, 2) maxilla, 3) fused premaxilla and maxilla, 4) autopalatine. The "premaxillae" of *Gigantura* and *Bathyleptus* have the following characteristics: they do not meet anteriorly, they attach anteriorly to the vomer and mesethmoid and posteriorly to the ectopterygoids, and they do not border on the posterior quarter of the upper jaw. Since the "premaxillae" do not border the upper jaw in its entirety, and since there is a separate ossification behind each "premaxilla," possible identifications (2) and (3) seem unlikely.

Consequently, the "premaxilla" appears to be the autopalatine, which would account for its anterior and posterior points of attachment to the skull, and which would also explain the apparent absence of palatines, as reported by Regan. If this interpretation is correct, the premaxillae have been lost by the Giganturidae. The small ossification behind the autopalatine is not likely to be premaxilla owing to its position; one would not expect the distal, free end of the bone to be retained while the proximal, articular end is lost. The small ossification behind the autopalatine is thus identified as the maxilla. This line of reasoning leads to the conclusion that the Giganturidae are sub-iniomes.

Non-identity of the Giganturidae with the iniomes, and identity with the sub-iniomes, is suggested also by the presence in *Bathyleptus* and in *Gigantura* of a gap between the hyomandibular and the preopercular; a muscle passes downward from the cranium through this gap to insert on the lower jaw. In none of the synodontoids has such an arrangement been noted, but there is a similar gap and muscle in *Esox lucius* and in *Argentina* (placed by Berg, 1940, in the Clupeiformes). It would be interesting to learn how many teleost groups have this muscle, and whether it may be of any phylogenetic significance.

The Giganturidae are considered here as representing an order Giganturoidea characterized as follows: upper jaw bordered by autopalatines and maxillae; premaxillae absent; maxillae not attached to skull; anterior myodome absent, posterior myodome present; orbitosphenoid, opisthotics, parietals absent; suspensorium directed backward as an evenly-curved arch; a lower jaw muscle passing through the preoperculo-hyomandibular gap: pectoral girdle free of skull and lacking posttemporal, supracleithrum, cleithrum and mesocoracoid; pelvic girdle absent; ventral parts of hyoid and branchial arches, including branchiostegal rays and symplectic, absent; pseudobranch, three holobranchs, one hemibranch; no gill rakers; pectoral fin base projects into gill chamber.

The relationship of the Giganturoidea to other teleosts is vague. It seems likely, however, that they belong somewhere between the esocoid members of the Isospondyli and the synodontoid members of the Iniomi.

Considering now the relationships of the Giganturoidea to higher teleost groups, Regan (1925) suggested they may be a

specialized offshoot from a line that led to the gulper eels, order Lyomeri (= Saccopharyngiformes). The magnificent studies of Tchernavin (1947a, 1947b) on *Saccopharynx* and *Eurypharynx* indicate many trenchant differences between the Lyomeri and Giganturoidea; Lyomeri have no supraoccipital, a bone which is well developed in Giganturoidea; Lyomeri have a special abductor mandibulae muscle while Giganturoidea have the usual depressor mandibulae muscle; Lyomeri have five or six holobranchs while Giganturoidea have three; Lyomeri have a single kidney, whereas Giganturoidea have paired kidneys; in Lyomeri the pectoral muscles originate on the pericardium, but in Giganturoidea the pectoral girdle is not associated with the heart. Harry (1952) pointed out further that the luminous organ of the order Cetunculi (*Cetomimus*) is comparable only with the luminous organ of Lyomeri. It is also noteworthy that in Cetunculi (*Cetomimus*) as in Giganturoidea the pectoral girdle is free of the skull (see above for pectoral girdle of *Harpadon*) and the stomach is deeply pigmented while the intestine is not (Parr, 1929). The skull of *Cetomimus* as illustrated by Parr (1929) is topologically not too different from the Giganturoidea. In conclusion, the Giganturoidea may be a specialized offshoot of a line that led from a sub-iniomous group such as the esocoids toward the synodontoid iniomes, and this line later may have given rise to the Cetunculi and perhaps eventually to the Lyomeri.

Family GIGANTURIDAE

In the following account, unless otherwise noted, statements concerning *Gigantura* and *G. vorax* are based upon specimens of *G. vorax* having the following standard lengths: 65 mm. (Museum of Comparative Zoology No. 40706), 77 mm. (Museum of Comparative Zoology No. 35605), 116 mm. (American Museum of Natural History No. 20393), 156 mm. (Bingham Oceanographic Collection No. 3228). Full data for these will be given in "Fishes of the Western North Atlantic," volume 4.

Diagnosis. Mesopelagic teleosts. Eyes large, tubular, directed forward. Gape of mouth extends far behind eye. Pectoral fin bases above gill openings. Pelvic fins absent. Dorsal fin behind middle of body. No adipose fin. Anal fin either partly below or entirely behind dorsal fin. Caudal fin forked and middle rays of lower lobe lengthened. Fin rays unsegmented, some

branched. Anus beneath dorsal fin. Sharp, recurved, depressible teeth on autopalatines, dentaries, ectopterygoids and upper pharyngeals. A layer of mesenchymal jelly beneath skin. Scales absent. Luminous organs absent. Coloration silvery.

Upper jaw bordered by autopalatines and maxillae. Autopalatines joined to vomer and mesethmoid anteriorly and to ectopterygoids posteriorly. Maxillae not attached to skull, but buried in upper lip behind autopalatines. Premaxillae absent. Anterior myodome absent. Posterior myodome present. Basisphenoid, pterosphenoid (= alisphenoid) present. Cartilaginous endocranium persists beneath surface bones. Supraoccipital meets frontals. Orbitosphenoid, opisthotics, and parietals absent. Suspensorium directed backward in an evenly-curved arch. Anterior upper pharyngeals between suspensoria. Retractor muscles of posterior upper pharyngeals originate on vertebrae dorsal to stomach. Rami of lower jaw loosely connected at symphysis. Throat a distensible membrane. Preopercular a splint applied to lower two-thirds of suspensorium. A gap between preopercular and hyomandibular, through which a muscle passes. Opercular excluded from posterior edge of gill flap by subopercular. Pectoral girdle not attached to skull: posttemporal, supracleithrum, cleithrum and mesocoracoid absent. Pelvic girdle absent. Ventral parts of hyoid and branchial arches, including branchiostegal rays and symplectic absent. One post-hyoidean arch complete, supporting both sets of pharyngeal teeth. Pseudobranch, three holobranchs, and hemibranch present; no slit behind hemibranch. No gill rakers. Pectoral fin base projects into gill chamber. Kidney close behind pectoral girdle. Swimbladder absent. Vertebrae 30-31.

Two genera, *Gigantura* Brauer 1901 and *Bathyleptus,* described below.

Bathyleptus,[1] gen. nov.

Genotype. Bathyleptus lisae, sp. nov.

Diagnosis. Epiotics almost as large as supraoccipital. Pineal foramen present. Preethmoid cornua present. Supraorbital lateral line canal in a bony ridge running full length of each frontal. Pectoral girdle cartilaginous, with scapula, coracoid and four radials. Pharyngeal retractor muscles short and

[1] From the Greek *Bathos* = deep; *Leptos* = slender; in reference to the depth range and body shape.

slender, originating on fifth or sixth vertebra. Visceral arch supporting pharyngeal tooth-plates connects with strap of longitudinally striated muscle on ventral surface of esophagus. Gill openings and three holobranchs extend onto throat. Sinus venosus anterior to liver. Trunk vertebrae several times longer than wide. Trunk pencil-shaped. Caudal peduncle depth equal to or less than its width. Least caudal peduncle depth 29-51 in standard length.

Comparison with Gigantura. The diagnosis of *Gigantura* which is given below follows the form used for *Bathyleptus.* Since the two accounts are mutually exclusive it is unnecessary to present a side-by-side comparison of the genera.

Gigantura Brauer, 1901. The epiotics are considerably smaller than the supraoccipital. There is no pineal foramen. Preethmoid cornua are absent. The supraorbital lateral line canal is in a bony ridge on each frontal between the orbits but the ridges do not extend much posterior to the orbits. The pectoral girdle contains an ossified scapula, ossified coracoid, cartilaginous postcoracoid process, and four ossified radials; the fin-rays are inserted on the radials. The pharyngeal retractor muscles are long and robust, and originate on the 12th through 16th vertebrae. The visceral arch which supports the pharyngeal tooth-plates connects with a strap of transversely striated muscle on the ventral surface of the esophagus. The gill openings and gills are situated entirely above the jaws. The sinus venosus lies between the lobes of the liver. The trunk vertebrae are about as long as they are wide. The trunk is heavy and compressed. The caudal peduncle is at least 1.5 times deeper than it is wide. The least depth of the caudal peduncle is contained 11 to 16 times in the standard length.

Species. Three nominal species are placed in *Bathyleptus.* See the remarks on *Gigantura indica* Brauer and *Gigantura gracilis* Regan in the diagnosis of the following species.

Bathyleptus lisae, sp. nov.

Figure 1

Holotype. Scripps Institution of Oceanography No. H51-375; September 15, 1951; eastern Pacific north of Hawaii at 31°54′-31°36′N., 152°21′-152°03′W.; 1790 fathoms with 10-foot Isaacs-Kidd midwater trawl; R/V HORIZON, R. L. Wisner; 168 mm. standard length.

Paratype. Scripps Institution of Oceanography No. H51-377; September 23-24, 1951; eastern Pacific north of Hawaii at 31°01'-31°09'N., 127°39'-127°24'W.; 2140 fathoms with 10-foot Isaacs-Kidd midwater trawl; R/V HORIZON, R. L. Wisner; head crushed, about 127 mm. standard length.

Description. D *17*-18; *A* 14-*15*; P *37*-38; C *17*-18; vertebrae ca. 30-*31; 10* enlarged autopalatine teeth on each side; *2* ectopterygoid teeth on each side. Fin counts include all elements; italicized values are for the holotype.

Proportional measurements as per cent of the standard length (values for holotype italicized): head length to rear angle of jaws *13.7;* head width across sphenotics *6.0;* autopalatine length *8.7;* body width at dorsal origin *3.0,* 4.7; body width at middle of caudal peduncle *2.1,* 3.5; body depth at dorsal origin *3.6,* 6.3; least depth of caudal peduncle *2.0,* 2.4; snout to dorsal origin 53.6, *54.8;* snout to anal origin 72.4, *74.5;* snout to pectoral beginning *11.6;* length of dorsal base *16.1,* 19.7; length of anal base 8.7, *8.9;* length of pectoral base *6.0.*

Diagnosis. The new species somewhat resembles *Gigantura chuni indica* Brauer (1901) of the Indian Ocean and *Gigantura gracilis* Regan (1925) of the tropical Atlantic, both of which are herewith transferred to *Bathyleptus* since they have extremely shallow caudal peduncles. *Bathyleptus gracilis* may be a synonym of *B. indicus.* The new species differs from the others as follows: in *lisae* the anal fin is completely behind the dorsal fin whereas in *gracilis* and *indicus* it begins beneath the rear portion of the dorsal fin; in *lisae* the anal fin base is longer than the pectoral fin base whereas it is shorter than the pectoral fin base in *gracilis* (condition unknown for *indicus*); *lisae* has 37-38 pectoral fin-rays versus 39-41 in *gracilis* and 40-43 in *indicus.*

The new species is named after my wife, Lisa.

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VARIATION IN *PARAMYXINE*, WITH A REDESCRIPTION OF *P. ATAMI* DEAN AND *P. SPRINGERI* BIGELOW AND SCHROEDER

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No. 11 — *Variation in Paramyxine, with a Redescription of P. atami Dean and P. springeri Bigelow and Schroeder*

By R. Strahan and Y. Honma

Paramyxine is characterized by having six pairs of external branchial apertures, crowded together towards the posterior end of the branchial region. Consequently, the most anterior efferent branchial ducts are several times the length of the posterior ones (Fig. 2). These characters are sufficient to distinguish *Paramyxine* from *Myxine* and related genera (*Nemamyxine, Neomyxine*, and *Notomyxine*) which have only one pair of external branchial apertures, and from *Eptatretus* (= *Bdellostoma*) in which the efferent branchial ducts are of equal length. Two species have been described: *P. atami* Dean 1904, based on a single specimen from 494 m off Cape Manazaru in Sagami Bay, Honshū, Japan, and *P. springeri* Bigelow and Schroeder 1952, based on three specimens taken at 400-600 m in the Gulf of Mexico.

Matsubara (1937) threw doubts on the sufficiency of the description of the type genus and species by demonstrating a considerable degree of variation in a small collection of myxinids taken at about 275 m from Kumano Nada, S.E. of Kii Peninsula, Honshū, Japan. These specimens did not conform completely either to the generic or specific descriptions of *P. atami*, but they were far closer to this species than to any other known forms and Matsubara considered that his specimens were "referable to the above species, although discrepant in several characters" (p. 13). Matsubara was concerned mainly in demonstrating the variation in the arrangement of the branchial apparatus and the teeth, and has left no record of the relative body proportions of his specimens.

Okada et al. (1948a, b) handled almost 1,000 specimens of a myxinid from the commercial hag-fishery of Sado Strait, taken at a depth of 60-160 m, off Niigata, N.W. Honshū, Japan. These authors were more concerned with data of commercial value (sex ratio, weight-length ratio, etc.) than with taxonomic features, and, following Matsubara (1937), they regarded their specimens as referable to *P. atami* even though, for example, the length of the type specimen lay outside the range of their large sample.

Bigelow and Schroeder (1952) have described some features of a specimen from Suruga Bay, S.E. Honshū, Japan (U.S. Nat.

Mus. No. 161442) which they regard (again, in spite of some discrepancies) as referable to *P. atami* Dean. On the basis of this specimen, Dean's (1904) description of the type, and some data from Matsubara (1937), these authors came to the conclusion that their Gulf of Mexico specimens were sufficiently different from *P atami* to justify the erection of a new species *P. springeri* Bigelow and Schroeder 1952.

Strahan and Honma (1960), in a brief account of the hagfishery of Sado Strait, tabulated the mean body proportions of 50 specimens from a sample of some 500 myxinids collected off Teradomari, N.W. Honshū, Japan. We had overlooked Bigelow and Schroeder's (1952) paper and, somewhat uncritically, had followed Okada et al. (1948a) in regarding our material as typical *P. atami.* We wish now to re-examine the situation in the light of more detailed measurements of some 140 specimens, and with respect to the work of Bigelow and Schroeder.

The Teradomari Sample

The method of collection of the most recent sample has been described by Strahan and Honma (1960). All the specimens were taken on the night of 21/22 October, 1959, at a depth of about 100 m, about 8 miles offshore of Teradomari-machi (near Niigata City), N.W. Honshū, Japan. The animals were maintained in aquaria for 1-3 days and measured under urethane anaesthesia. After measurement, the pituitary glands were removed from the majority of the animals (this being the prime object of the expedition) and the bodies discarded. Some 50 specimens, preserved in formalin, were retained for later examination.

Hagfish are remarkably lacking in taxonomic features susceptible to quantitative formulation. External features that can be studied quantitatively are limited to the over-all length, the number of gill apertures and their position on the body, the position of the cloacal aperture, the number of slime glands and their distribution with respect to the gills and the cloaca. The caudal fin terminates ventrally at the posterior border of the cloaca, but the anterior limit of the dorsal caudal fin is not clearly defined. Similarly, the anterior limit of the ventral (anal) fin is difficult to define. Internal features of taxonomic value are the number and arrangement of the lingual teeth, and the number of gills.

Length. Specimens varied in length from 130 to 583 mm. Hitherto, the longest recorded specimen was the type, 550 mm

long. Matsubara's (1937) specimen was 475 mm long and Okada et al. (1948) did not record any individuals longer than 500 mm. The length frequency of the Teradomari collection is illustrated in Figure 1 and, for comparison, the length frequency histograms of Okada et al. (1948a) are included.

There is a slight difference in the mode of the length in June, August, and October (respectively, 325 mm, 316 mm, and 343 mm) but this may be without significance, particularly since the later measurements are separated by more than a decade from the earlier ones. However, there is a very suggestive increase, from June to October, in the relative frequency of very large individuals (400 mm and more in length).

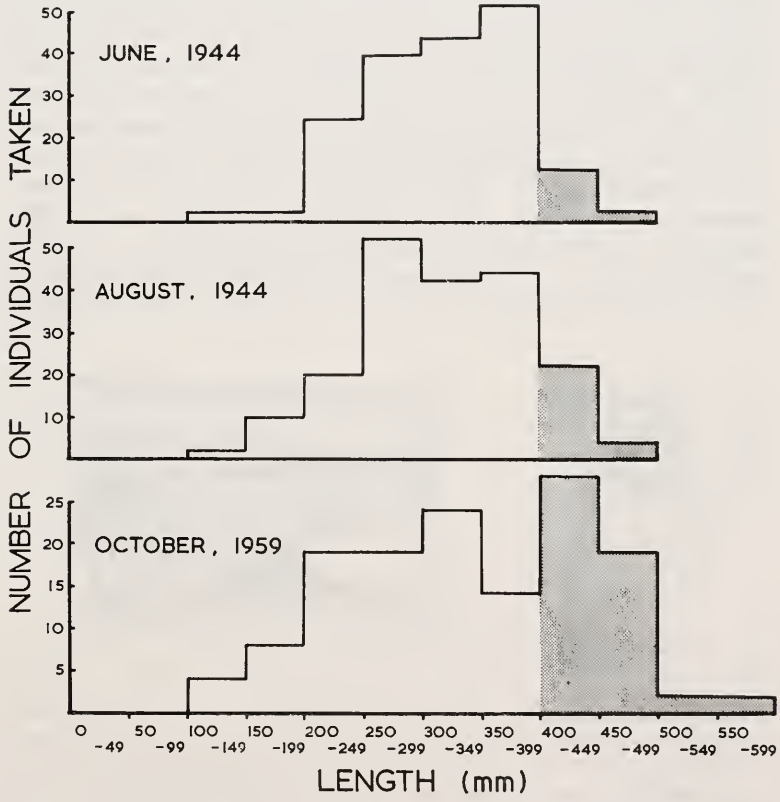

Fig. 1. Length-frequency histogram, *P. atami* taken in the vicinity of Niigata, Japan. Data for June and August, 1944, taken from Okada et al. (1948a). Shaded portions of histogram indicate relative numbers of individuals over 400 mm in length.

Okada et al. (1948b) concluded that spawning occurs off Teradomari mainly in April and May, but that it may extend into August. In late October we found many females with apparently mature eggs. In view of the extreme uncertainty regarding the spawning season (if any) of *Myxine glutinosa* and *Eptatretus stouti* despite extensive and prolonged investigations (see Bigelow and Schroeder, 1948; Conel, 1931), we feel that it is better to leave the question open for the time being.

Branchial system. Dean (1904) defines the genus *Paramyxine* entirely on the branchial system: "Hyperotretes with branchial apertures ventrad of sacs. Ectal branchial ducts of distinctly unequal length, the most anterior several times the length of the most posterior. The duct of the most anterior gill opening at the surface opposite the fourth (or fifth) gill sac. Openings of branchial ducts drawn close together and compressed transversely, that of the ductus oesophagoeus, however, longitudinally, the latter aperture of large size, its length equalling that of the sum of the interspaces of several gills. Transverse constrictor muscles of the branchial region developed as a distinct element in the region of the hindmost branchial sacs." His diagnosis of the species, *P. atami*, adds that there are six gills, that the ectal duct of the most anterior gill is three or more times the length of the most posterior, that the base of the tongue

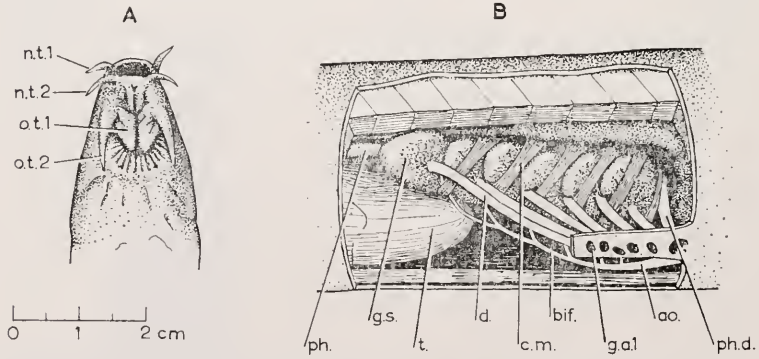

Fig. 2. A. Ventral view of head of *P. atami*, 460 mm long. B. Dissection of left branchial region of *P. atami*, 530 mm long. Abbreviations: *ao.*, ventral aorta; *bif.*, bifurcation of aorta (right branch not shown); *c.m.*, branchial constrictor muscles; *d.*, efferent branchial duct; *g.a.1.*, first gill aperture; *g.s.*, first gill pouch; *n.t.1,2*, first and second nasal tentacles; *o.t.1,2*, first and second oral tentacles; *ph.*, pharynx; *ph.d.*, pharyngocutaneous duct; *t.*, base of 'tongue' muscle.

muscles lies between the third pair of branchial sacs, and that the gill apertures are white against a purplish skin.

The general arrangement of the gill-pouches and ducts in a specimen from Teradomari is shown in Figure 2. It can be seen that this agrees with Dean's description in many respects. However, as Matsubara (1937) noted, there is considerable variation in the position of the posterior end of the lingual musculature. In the individual depicted, this lies between the second pair of gill pouches, but in different individuals its position varies from the first to the fourth gills.

The position of the gill apertures was not recorded by Dean (1904) nor by Matsubara (1937), but we agree with Bigelow and Schroeder (1952) in regarding this as taxonomically significant, although variable. In Tables 1 and 2 the distance from the anterior extremity of the body to the first and to the sixth gill slit is set out as a function of the total length of the animal. There is a definite, though slight, tendency for the branchial

Table 1. Position of the 1st gill aperture in Paramyxine atami from Teradomari. Based on 139 specimens.

Total length (mm)	Snout to 1st gill aperture (% of total length)																Arithmetic mean ± S.D.
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
100 - 199								2	7	3							29.0 ± 0.6
200 - 299					1	2	3	8	18	4	0	0	1	0	0	1	28.8 ± 1.8
300 - 399						4	6	15	10	3							28.1 ± 1.0
400 - 499	1	0	0	0	1	6	12	10	15	2							27.7 ± 1.6
500 - 599						2	2										26.5 ± 0.5
All	1	0	0	0	2	14	23	35	50	12	0	0	1	0	0	1	28.2 ± 1.6

Table 2. Position of the 6th gill aperture in Paramyxine atami from Teradomari. Based on 139 specimens.

Total length (mm)	Snout to 6th gill aperture (% of total length)																Arithmetic mean ± S.D.
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	
100 - 199								1	6	3	2						32.5 ± 0.7
200 - 299					1	1	3	3	12	15	1	1	0	0	0	1	32.3 ± 1.7
300 - 399							6	11	10	9	1	1					31.8 ± 0.4
400 - 499	1	0	0	0	1	2	8	9	16	8	2						31.3 ± 1.7
500 - 599							2	0	1	1							31.2 ± 1.4
All	1	0	0	0	2	3	19	24	45	36	6	2	0	0	0	1	31.7 ± 1.5

region to occupy a relatively more anterior position in larger individuals than in shorter ones.

Matsubara (1937) and Strahan and Honma (1960) have drawn attention to the very considerable variation in the arrangement of the external branchial apertures, examples of which are shown in Figure 3. The 12 individuals depicted constitute a random sample which, although it is too small to indicate the relative frequency of particular variations, indicates their type and degree. Matsubara (1937) found only one of his 14 preserved specimens from S. E. Honshu in which the gill apertures were arranged in regular linear series. The remainder showed roughly the same degree of variation as those depicted here. Bigelow and Schroeder (1952) had at their disposal only one specimen of *P. atami* and this, like Dean's type specimen,

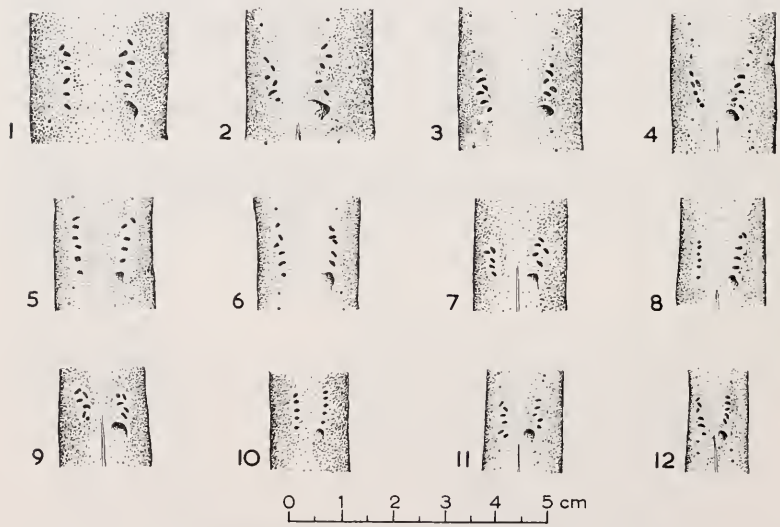

Fig. 3. Variation in arrangement of gill apertures in *P. atami*. Camera lucida drawings of formalin-preserved specimens.

had the gill openings regularly and evenly aligned. Commenting upon Matsubara's observations, these authors suggest that the irregularities may be due to muscular contraction. We are convinced that this is not so, since we have observed quite irregular arrangements in heavily anaesthetised animals. On the other hand, we agree with Matsubara (1937) in his suggestion that the outline of the apertures is liable to change during

preservation. In the living animal, the apertures may be more or less circular, triangular, or elongately oval, but the outline is smoothly convex. After preservation in formalin, the more elongate apertures may develop crenellations and become crescentic. However, if such specimens are placed for a time in water, the turgor developing from osmotic inflow restores a condition similar to that in life. The specimens depicted in Figure 3 were so treated.

Dean (1904) regarded the transverse orientation as a generic character. In common with Matsubara (1937) and Bigelow and Schroeder (1952), we find that the variation is too great to sustain this opinion. Similarly, we must reject Dean's criterion of a longitudinally elongated aperture to the pharyngo-cutaneous duct ("ductus oesophagoeus"). The pharyngo-cutaneous duct and sixth branchial aperture communicate with a shallow common depression, partially covered by a more or less semicircular fold of skin, and directed postero-mesially. The arrangement is not particularly variable and we have found no example of a markedly longitudinal depression. We can, however, confirm that the gill apertures have unpigmented borders.

In a number of individuals (Fig. 3, Nos. 7 and 10) there are only 5 gill apertures on the right-hand side of the body, and we have seen one individual in which there were only 4. The left-hand side is less variable in this respect, although one individual was found with 7 apertures on this side, due to separate opening of the 6th efferent branchial duct and the pharyngo-cutaneous duct. The existence of 5 apertures does not necessarily imply that there are only 5 gill pouches. Dissection of three individuals with 5 apertures on the left side revealed 5 gill pouches in one individual and 6 in the other two, the latter having one of the apertures shared by two adjacent ducts.

The cloaca. The cloaca is slit-like, as in *Myxine,* and surrounded by slightly swollen lateral lips. The ventral caudal fin arises immediately posterior to the cloaca, and we have therefore used the posterior border of the cloaca as a measurable landmark for this structure. The ventral (anal) fin terminates just anterior to the cloaca.

As can be seen from Table 3, the cloaca occupies a relatively more posterior position in longer individuals. Since the branchial region is relatively more anterior and the cloaca relatively more posterior in longer specimens, the length of the abdomen is quite markedly increased, and this is consequently a poor taxonomic character.

Slime glands. The slime glands, where they occur, are segmentally arranged, one per myotome. The linear series begins at the fourth or fifth myomere and extends back to the myomere immediately in front of the 1st branchial aperture. A second series begins at the level of the first postbranchial myomere and continues to the region of the cloaca where there is a gap, representing from one to four myomeres, after which a third series continues for about ten myomeres up to the region of the caudal heart. Thus, the slime glands may be divided into a prebranchial, an abdominal, and a caudal series.

Table 3. Position of the posterior border of the cloaca in Paramyxine atami. Teradomari sample. Based on 136 specimens.

Total length (mm)	Snout to posterior border of cloaca (% of total length) 81 82 83 84 85 86 87 88 89 90 91 92	Arithmetic mean ± S.D.
100 - 199	6 0 5	86.9 ± 1.0
200 - 299	1 0 0 0 1 7 8 17 3	87.2 ± 1.4
300 - 399	3 1 7 16 9 2	87.9 ± 1.2
400 - 499	7 19 15 3 1 1	88.5 ± 1.0
500 - 599	1 0 3	88.5 ± 0.8
All	1 0 0 0 4 14 23 57 30 5 1 1	87.8 ± 1.1

The mean values for the three series and for the total number are set out in Table 4. There is no correlation between the number of slime glands and the total length. This is perhaps to be

Table 4. No. of slime glands in left side of body of Paramyxine atami from Teradomari. Based on 123 specimens.

Total length (mm)	Mean No. of Slime glands			
	Prebranchial Series	Abdominal Series	Caudal Series	Total No.
100 - 199	18.8 ± 0.9	45.0 ± 1.4	11.3 ± 0.8	75.7 ± 2.0
200 - 299	18.6 ± 1.3	44.9 ± 2.2	11.0 ± 1.0	74.5 ± 2.6
300 - 399	18.9 ± 1.5	44.6 ± 1.9	10.9 ± 0.9	74.7 ± 2.5
400 - 499	18.9 ± 1.0	45.1 ± 1.4	10.8 ± 0.9	74.9 ± 2.2
500 - 599	19.3 ± 0.9	47.3 ± 0.9	11.5 ± 1.1	77.7 ± 1.3
All	18.8 ± 1.2	45.0 ± 1.9	10.9 ± 1.0	74.9 ± 2.6

expected if the number of slime glands is determined by the number of myomeres. The total number of slime glands is fairly constant, 95 per cent of the specimens examined having a total number of slime glands falling within two standard deviations of the arithmetic mean (71-79). The division of the glands into three linear series is more variable. Of the sample of 123 individuals, only 3 have the arrangement suggested by the means of each series (prebranchials 19: abdominals 45: caudals 11), but 78 (63%) fall within one standard deviation of these means (prebranchials 18-20: abdominals, 43-47; caudals 10-12), and 121 (98%) fall within two standard deviations (prebranchials, 16-21: abdominals 41-49: caudals 9-13).

Caudal fin. In our original description (Strahan and Honma, 1960, p. 29) we stated that "the dorsal caudal fin has no clearly-definable origin, but may be said to arise at approximately the level of the anterior border of the cloaca." However, Bigelow and Schroeder (1952) state that their specimen of *P. atami* has a dorso-caudal fin extending as far forward as the 6th pair of gill apertures, although it is only a low ridge. These authors also draw attention to Matsubara's (1937) illustration, which shows a dorsal fin of about the same height as the ventral fin, extending forwards to what they estimate as "one-third to one-half the distance from the level of the cloacal pocket toward the level of the 6th pair of gill openings," i.e., about 60 per cent of the length of the body from the snout. Unlike the ventral (anal) fin, the dorsal caudal fin is supported by fin-rays, and its limits may be specified in terms of the distribution of these structures. We skinned a small number of specimens and found a series of dorsal fin rays extending anteriorly to about 65 per cent of the body length from the tip of the head (see Table 5).

The difference between the apparent and real origin of the dorsal caudal fin, i.e., the position of the most anterior fin-ray and the point at which the fin becomes obvious as a thin membrane distinct from the rounded contour of the body, is due to several factors. The fin-rays anterior to the level of the cloaca are short and inclined strongly towards the horizontal. Between them and the skin of the fin is considerable fatty connective tissue which masks the discontinuity between the fin and the body proper. It is unlikely that this part of the fin is very much more prominent in life, for the skin here is thick and tough.

The caudal fin is continuous around the tail and extends forward ventrally as far as the posterior border of the cloaca. The fin-rays in the ventral part of the caudal fin are unbranched, in contrast to those in the dorsal and terminal part.

Table 5. Real and apparent anterior limits of the dorsal fin, based on 8 skinned specimens of Paramyxine atami.

Total length	Apparent origin Distance from snout		Most anterior fin-ray Distance from snout		Number of rays
(cm)	(cm)	% Total length	(cm)	% Total length	
139	112	80	93	67	-
191	160	84	130	68	51
278	225	81	175	63	53
291	241	83	186	64	56
295	245	83	183	62	63
310	254	82	207	67	48
353	295	84	228	65	61
355	300	85	227	64	66
Mean ± S.D.		83 ± 1		65 ± 1	57 ± 7

Bigelow and Schroeder (1952) found a difference in the configuration of the ventral border of the caudal fin in *P. atami* and *P. springeri*. They state (p. 4) that it is "nearly straight in all three of the Gulf of Mexico specimens while it is pictured as moderately convex in the two Japanese specimens of *atami* which have been illustrated (Dean 1904, pl. 1, fig. 3; Matsubara 1937, pl. 1, fig. A), likewise in the National Museum specimen of *atami* (compare Fig. 5 with Fig. 6)." We do not find this to be a specific character. In Figure 4, we have depicted the caudal fins of ten randomly-selected individuals. These show slight convexity and concavity, but are no less straight than that of *P. springeri* (Fig. 4, no. 11). The posterior part of the fin has a white border, one to two mm deep.

The ventral fin. In anaesthetized animals, it is difficult to determine the anterior limit of the ventral (anal) fin. The shrinkage caused by preservation renders the fin more conspicuous, but it does not permit very accurate localisation of the junction between the thin fin and the thick ridge running along the mid-ventral surface of the abdomen. In a sample of 42 preserved specimens, we estimate the anterior border of the

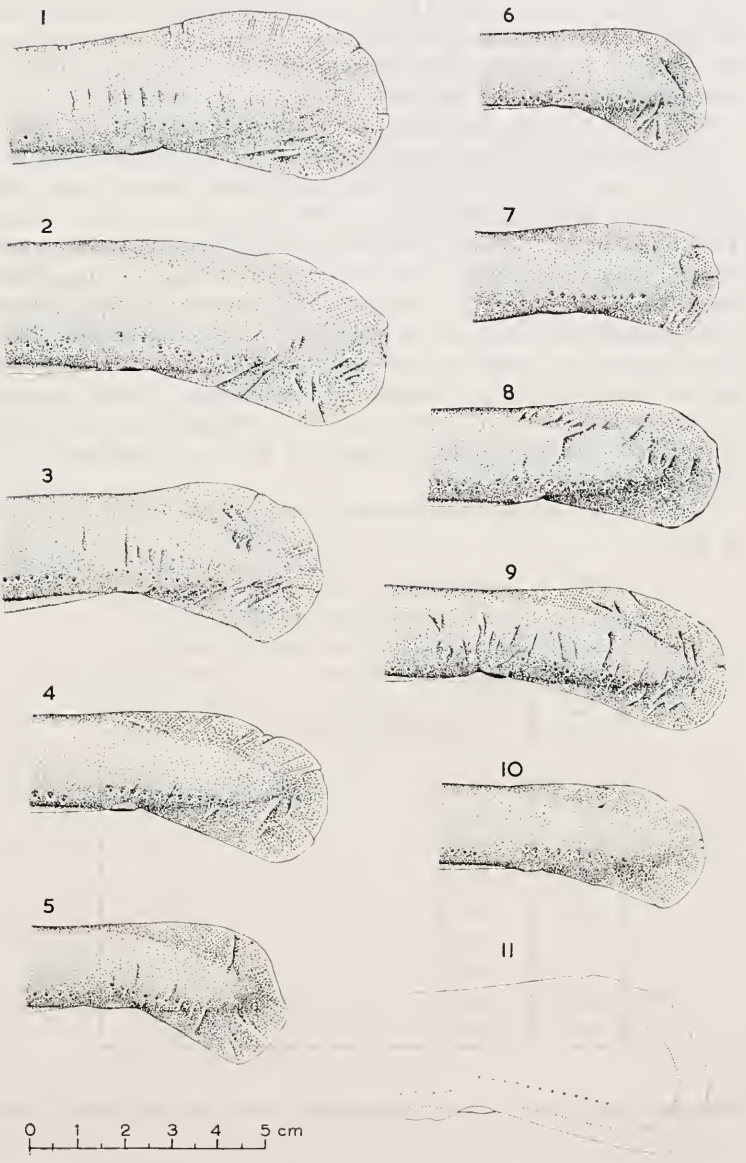

Fig. 4. Contour of the caudal fin in *Paramyxine*. Nos. 1-10, *P. atami*, camera lucida drawings of formalin-preserved material. No. 11, *P. springeri* (after Bigelow and Schroeder, 1952). Note variation in the arrangement of the slime glands.

ventral fin to be situated 47.3 + 2.7 per cent of the total length of the body from the anterior tip. This value ranges from 39 per cent to 54 per cent; but we find no correlation between this and the length of the body.

The lingual teeth. The procedure for dissecting the pituitary of the animal involved splitting the dental skeleton longitudinally. The teeth of the left side only were counted and thus we have no data on the degree to which asymmetry may occur. The teeth were counted under a binocular microscope, care being taken to lift away the skin fold covering the outermost teeth of each row. The frequency distribution of the various combinations of teeth on the outer and inner combs (see Table 6) is much the same as that published in our earlier paper, but is based on a larger number of specimens. It may be noted that the range does not come near to including 13 outer: 12-13 inner, which is the dental formula of the type specimen of *P. atami*.

There is no correlation between total length and the number of teeth.

Table 6. Arrangement of lingual teeth in Paramyxine atami from Teradomari. Based on 109 individuals.

Number of teeth		Number of	Percentage of
Outer row	Inner row	individuals	individuals
8	10	1	1
9	9	13	12
9	10	9	8
10	9	10	9
10	10	55	50
11	11	4	4
11	9	2	2
11	10	9	8
11	11	5	5
12	10	1	1

Differences between specimens from the east and west coasts of Japan

Records of the occurrence of *Paramyxine* have been collated by Strahan and Honma (1960). On the Pacific coast of Honshū it has been recorded from Aomori Province (Matsubara, 1955),

Ibaragi Prefecture (Asano, 1956), Sagami Bay (Dean, 1904), Suruga Bay (Bigelow and Schroeder, 1952), Kii Peninsula (Matsubara, 1937), and Kōchi Prefecture (Kamohara, 1952). On the east coast of Honshū, there are records from the vicinity of Niigata (Okada et al., 1948a, b; Strahan and Honma, 1960), and from San-in District (Mori, 1956). Mori (1952) includes *P. atami* in a check-list of Korean fishes.

There seems to have been no attempt to compare these specimens in detail with the type, except in the case of Bigelow and Schroeder who, like Dean, were limited to one specimen. Since the Teradomari sample differs in several characteristics from the type and from the U.S. National Museum specimen, both of which are from the east coast of Honshū, we tried to get a sample of *Paramyxine* from the Pacific coast of Japan, but have been able to obtain only five specimens, from Kanbara, in Suruga Bay. These are similar in body proportions to the U.S. National Museum specimen (also from Suruga Bay) and they have been grouped together with it for comparison with the Teradomari sample, the type, and the specimens from the Gulf of Mexico (Table 7).

Table 7. Taxonomic characters of Paramyxine populations from the east and west coasts of Honshu, and from the Gulf of Mexico.

Character	Western Japan	Eastern Japan		Gulf of Mexico
	Teradomori[1] (120 - 140)	Suruga Bay (6)	Sagami Bay (1)	(3)
Snout to 1st gill aperture (% T.L.)	28.2 ± 1.6	26.6 ± 1.0	25.5	23.1 ± 0.4
Snout to 6th gill aperture (% T.L.)	31.7 ± 1.5	29.9 ± 1.2	27.9	26.6 ± 1.0
Snout to post border cloaca (% T.L.)	87.8 ± 1.1	87.1 ± 0.3	85.5	85.2 ± 1.7
No. prebranchial slime glands	18.8 ± 1.2	16.6 ± 1.1	17-20 ?[2]	17.3 ± 1.7
No. abdominal slime glands	45.0 ± 1.9	45.5 ± 1.1	58 ?[2]	52.3 ± 5.5
No. caudal slime glands	10.9 ± 1.0	9.0 ± 1.1	10 ?[2]	12.2 ± 1.0
Total no. slime glands	74.9 ± 2.6	71.0 ± 2.1	?[2]	86.0 ± 5.6
Mean no. teeth, outer row	10.0 ± 0.7	11.5 ± 0.5	13	13.5
Mean no. teeth, inner row	10.0 ± 0.6	11.5 ± 0.5	12.5	11.5

1. Figures in brackets under place names indicate size of sample.
2. Dean's two illustrations are not in agreement with each other.

With respect to all the characters set out in Table 7 (except the number of abdominal slime glands), the specimens from Suruga Bay are significantly different from the Teradomari sample (difference between the means is of the order of three times the sum of the standard error of the means). In spite of

the small size of the Suruga Bay sample, this indicates a biological difference between the two populations, although this is probably not so great as to warrant sub-specific distinction, since the joint non-overlap (Mayr, Linsley and Usinger, 1953) of the most divergent character (no. of lingual teeth) does not exceed 89 per cent.

Data on the type specimen are rather unreliable. The only measurement given by Dean (1904, p. 14) is the total length (about 550 mm). Bigelow and Schroeder (1952) attempted to derive the dimensions from Dean's figures, but the figures themselves are suspect, particularly with respect to the slime glands, which Dean regarded as too variable to be of taxonomic value. The measurements given for the type specimen in Table 7 are calculated from Dean's (1904) text-figure 2 and plate I, fig. 3. Insofar as any reliance can be placed on them, they indicate that the branchial region is even more anterior than in the Suruga Bay specimens, while the cloaca is even more anterior than in the Teradomari sample. The number of abdominal slime glands appears to be considerably greater in his specimen than in other Japanese *Paramyxine*. Nevertheless, there is insufficient evidence to separate this single specimen from others that we have examined. The Teradomari sample included a specimen with body proportions fairly similar to the type (250 mm long; snout to 1st gill aperture, 26%; snout to 6th gill aperture, 28%; snout to posterior border of cloaca, 89%; pre-branchial slime glands, 16; abdominal slime glands, 51; caudal slime glands, 11), so it seems that the type may be regarded as atypical, but within the range of variation which has been demonstrated.

The Validity of P. springeri

Once the type description is questioned, the validity of the separation of *P. springeri* from it must also be reviewed. However, reference to Table 7 shows that the specimens from the Gulf of Mexico differ from the Teradomari and Suruga Bay populations even more than they do from the type specimen. There is a significant difference between the means of all the characters tabulated for the Teradomari and American forms, and the percentage of non-overlap is high for many of the characters (snout to 1st gill aperture, snout to 6th gill aperture, total number of slime glands, and number of lingual teeth), exceeding 96 per cent. This, in itself, is probably only enough

to justify separation into subspecies. There is, however, a further difference between *P. atami* and *P. springeri* which permits a clear separation. This is the presence in *P. springeri* and the absence in *P. atami* of slime glands in the branchial region. As mentioned above, the prebranchial series of slime glands in *P. atami* is clearly separated from the abdominal series by a gap in the region of the branchial apertures. In *P. springeri* there is a short series of glands in the branchial region, running parallel to, and on the ventro-mesial side of the line of the gill apertures. In the three specimens of *P. springeri* which have so far been described, the number of glands in the "branchial" series varies from 3 to 6.

Discussion

Dean (1904, p. 18) states, "The wide range in the variational characters in species of myxinoids has long been appreciated, in the matter, for example, of the number of gills and 'teeth' and in the proportions of body regions and fins. My own observations lead me to the belief that in the case of myxinoids it is peculiarly necessary to base specific determinations upon the average characters of as great a number of individuals as practicable." Similar views have been expressed by Ayers (1894, *fide* Worthington) and Worthington (1905), who worked on the Californian *Eptatretus*, and by Bigelow and Schroeder (1948) in their review of the reputed species of *Myxine*. However, no authors have hitherto presented a simple analysis of variation within a myxinid population, expressed in terms of mean values of quantitative characters and the standard deviations of these means. Without such treatment, and quantitative consideration of the degree of overlap of different populations, there is very little that can be usefully said on the subject.

Our analysis makes it clear that there is a significant difference between *P. atami* from Teradomari and *P. atami* from Suruga Bay. From this, we have deduced the existence of an eastern and a western form of the species. Proof of this would require more widespread sampling, to determine, for instance, whether the populations intergrade with each other around the north and south coasts of Honshū, or whether there is discontinuous variation. There is a possibility of a cline extending from the Sea of Japan to the Gulf of Mexico. It is dangerous to assume this on three samples, two of which are rather small, but examination of Table 7 suggests that such a cline may involve

a progressive shortening of the prebranchial region and an increase in the number of lingual teeth from west to east over the range of the genus.

The type specimen of *P. atami* is incompletely described, and the diagnosis of the genus and species has been shown to be at fault in several respects. We therefore propose a further description of the genus and species, and a simplified description of *P. springeri*. The latter is based entirely upon the excellent description of Bigelow and Schroeder (1952) and differs from it mainly in selection of those characters which we regard as taxonomically significant.

Paramyxine Dean 1904

Myxiniformes characteristically with 6 gills with separate efferent branchial ducts of distinctly unequal length, the most anterior being more than twice the length of the most posterior, opening separately to the exterior, except for the most posterior on the left side, which opens into the same external aperture as the pharyngo-cutaneous duct. External branchial apertures lying close together in the posterior third of the branchial region, the series on the two sides converging rearwards in a linear or irregular arrangement.

Rostral flap above nasal aperture wider than long, nasal aperture relatively larger in diameter than in *Myxine*. Distal ends of second pair of oral tentacles bluntly rounded.

Dorsal caudal fin apparently originates at level of cloaca (but fin rays may extend farther forward), continuous around posterior tip of body to posterior border of cloaca, ventral edge of fin more or less straight. Ventral (anal) fin extends from anterior border of cloaca to about 40 per cent of the length of the body from the snout.

Body darker on back and sides than ventrally, edges of caudal and anal fin and tips of tentacles paler than surrounding skin. Branchial apertures with white borders. Distinct pale patch over region of eye.

Up to about 60 cm in length.

Paramyxine atami Dean 1904

Six gills (rarely five on right side), external branchial apertures in two irregular (rarely regular) rows on ventral surface. Snout to first gill aperture 28.2 $\pm$ 1.6 per cent of total length

(western form) or 26.6 ± 1.0 per cent (eastern form). Snout to posterior border of cloaca 87.8 ± 1.1 per cent of total length (western form) or 87.1 ± 0.3 (eastern form). Slime glands 18.8 ± 1.2 prebranchial, 45.0 ± 1.9 abdominal, 10.9 ± 1.0 caudal (western form). Slime glands 16.6 ± 1.1 prebranchial, 45.5 ± 1.1 abdominal, 9.0 ± 1.1 caudal (eastern form). Total number slime glands 74.9 ± 2.6 (western form) or 71.0 ± 2.1 (eastern form). No slime glands in region of branchial apertures. Lingual teeth, 10 ± 0.7 outer, 10 ± 0.6 inner (western form) 11.5 ± 0.5 outer, 11.5 ± 0.5 inner (eastern form).

Color, purplish-brown dorsally and laterally, grey ventrally. Length, up to 58 cm. Coastal waters of Honshū (Japan), Korea.

Paramyxine springeri Bigelow and Schroeder 1952

(Simplified Description for Comparison with *P. atami*)

Six gills, external branchial apertures in two rather regular rows on ventral surface. Snout to 1st gill aperture 23.1 ± 0.4 per cent of total length. Snout to posterior border of cloaca 85.2 ± 1.7 per cent. Slime glands 17.3 ± 1.7 prebranchial, 52.3 ± 5.5 abdominal, 12.2 ± 1.0 caudal. Total number of slime glands 86.0 ± 5.6. Slime glands on each side, ventro-mesially to external branchial apertures. Lingual teeth 13-14 outer, 11-12 inner. Color, greyish-brown. Gulf of Mexico.

Supplementary Note

Teng (1958) has recently described a new species, *P. yangi*, eight specimens of which have been obtained from fish markets in Kaohsiung, Taiwan, and are assumed to have been caught in waters to the southwest of Taiwan. *P. yangi* is characterised by having only 5 pairs of gills and external branchial apertures, arranged irregularly as in *P. atami*. The head is longer than in *P. atami* or *P. springeri*. A summary of the major characteristics is given below.

	Mean and Standard Dev.	Range
Total length (T.L.)	229±6 mm	(198-250 mm)
Snout to 1st branchial aperture (% T. L.)	31.7±1.3	(28.9-32.9)
Snout to 5th branchial aperture (% T.L.)	33.3±1.0	(30.7-34.9)
Snout to post. border of cloaca (% T.L.)	86.0±1.8	(81.2-87.6)
No. prebranchial slime glands	18.1±1.0	(17-20)
No. abdominal slime glands	37.1±1.5	(35-40)
No. caudal slime glands	8.6±1.1	(8-10)
Total no. slime glands	63.8±2.8	(60-69)

Key to species of *Paramyxine*

1a. Five pairs of gills; snout to 5th branchial aperture about 33% of total length; about 65 slime glands on each side; number of abdominal slime glands approximately twice the number of prebranchial slime glands; slime glands absent between 1st and 5th branchial apertures; 9-10 lingual teeth in internal row, 9-10 in external row; up to 250 mm in length. ..... *yangi* Teng, 1958. Taiwan.

1b. Six pairs of gills.

2a. Snout to 6th branchial aperture about 30% of total length; about 75 slime glands on each side; number of abdominal slime glands approximately 2.5 times the number of prebranchial slime glands; slime glands absent between 1st and 6th branchial apertures; 9-10 lingual teeth in internal row, 9-10 in external row; up to 583 mm in length. ..... *atami* Dean, 1904. Japan.

2b. Snout to 6th branchial aperture about 27% of total length; about 85 slime glands on each side; number of abdominal slime glands approximately 3 times the number of prebranchial slime glands; 3-6 pairs of slime glands between 1st and 6th branchial apertures; 11-12 lingual teeth in internal row, 13-14 in external row; up to 590 mm in length. ..... *springeri* Bigelow and Schroeder, 1952. Gulf of Mexico.

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SUMMARY

Variation in the taxonomic characters of *Paramyxine atami* Dean from the eastern and western coasts of Japan is described. These populations differ significantly (in the position of the branchial region, the number of prebranchial and caudal slime glands, and the number of lingual teeth), but not sufficiently to

rank as subspecies. The type specimen is not typical of either population and appears to be an unusual specimen. Certain points in the original definitions of the genus and species are invalid and further descriptions are given. *P. springeri* Bigelow and Schroeder, from the Gulf of Mexico, is found to be taxonomically distinct from *P. atami,* particularly in possessing slime glands in the branchial region. A simplified diagnosis of of *P. springeri* is given. A note on the recently described species, *P. yangi* is appended, with a key for separation of the three species of *Paramyxine*

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ABYSSAL MOLLUSKS FROM THE SOUTH ATLANTIC OCEAN

By Arthur H. Clarke, Jr.
National Museum of Canada

With Four Plates

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No. 12 — *Abyssal Mollusks from the South Atlantic Ocean*[1,2]

By Arthur H. Clarke, Jr.

INTRODUCTION

During the twelfth cruise of the Lamont Geological Observatory research vessel VEMA (see Ewing and Heezen, 1956) made in 1957, extensive biological and geological explorations were carried out in the Argentine Basin and off the west coast of Africa from the Agulhas Basin to the Guinea Basin. Sixteen successful bottom trawls were made in these regions, fourteen of which were from abyssal depths. In 1958, the fourteenth cruise of the VEMA again allowed opportunities to trawl in the South Atlantic, and eleven bottom samples were taken from the area between South Georgia and the Cape of Good Hope. Eight of these were also from abyssal depths. The numerous mollusks collected are nearly all quite different from North Atlantic forms, and many new species are present. Several of these are described on the following pages.

A summary of information regarding the trawling stations is given in the tables below. At station 12, a bottom trawl with an opening 3 meters wide was employed but at each of the other stations a 1 meter trawl was used. Both trawls were equipped with a fine mesh nylon net which retains all benthic animals larger than small foraminifera. At each station the trawl was in contact with the bottom for approximately 30 minutes.

R/V VEMA Abyssal Trawling Stations in the South Atlantic Ocean

L.G.O. Station No.	Latitude	Longitude	Corrected Depth (fathoms)
12	38°58.5′ S	41°45′ W	2805
14	30°14.9′ S	13°03′ E	1703
15	28°25.2′ S	8°28.5′ E	2770
16	25°33′ S	12°27′ E	1660
18	23°00′ S	08°11′ E	2262
19	22°58.5′ S	07°00′ E	1510
20	22°41′ S	03°16′ E	2767
22	5°53.5′ S	09°51.5′ E	1675
23	6°19.3′ S	08°18.5′ E	2193

[1] This paper is part of a doctoral thesis accepted by Harvard University in May, 1960.

[2] Contribution No. 503, Lamont Geological Observatory (Columbia University), Palisades, New York.

25	4°23.9′ S	00°18′ W	2315
46	55°19′ S	37°57′ W	2030
47	55°29′ S	37°57′ W	2054
48	56°37′ S	34°38′ W	1902
49	56°43′ S	27°41′ W	1497
50	57°39′ S	13°37′ W	2064
51	45°34′ S	06°02′ E	2507
52	41°03′ S	07°49′ E	2711
53	36°34′ S	14°08′ E	2670
54	34°35′ S	17°31′ E	993
57	29°44′ S	37°15′ E	2727
212	47°57.5′ S	48°03′ W	3334

Additional information is available for some of the stations, and since it may be significant it is included below.

Supplementary Information on R/V VEMA
Stations in the South Atlantic Ocean

L. G. O. Station No.	Surface Sediment	Bottom Temp. (°C.)	Oxygen (ml/L.)	Dominant Animal Groups
12	red clay			crustaceans, mollusks
14	foraminifera	2.43	4.8	crustaceans, echinoderms, worms
15	white clay + Mn nodules			worms
16	foraminifera			echinoderms, crustaceans, nematodes
18	foraminifera	1.35		
19	foraminifera			
20	red clay	2.5	3.4	
22	greenish lutite			worms, crustaceans
23	red clay	0.76		worms, crustaceans
25	foraminifera			crustaceans

In addition to giving the localities in terms of distance and direction from selected points on the land, on the following pages ocean basins are also cited. Basin terminology follows that used by Sverdrup, Johnson, and Fleming (1942). Such a procedure is considered useful in the present study, and it is hoped that it will be adopted generally in other works dealing with the mollusks of the open sea.

ACKNOWLEDGMENTS

Prof. Maurice Ewing generously provided the opportunity to study the mollusks on which this report is based. Much additional material for comparison was freely made available by Drs. William J. Clench and Harald A. Rehder. Dr. Clench and Dr. Ruth D. Turner also read the manuscript. The research was conducted at Harvard University and was supported by the Lamont Geological Observatory by means of Rockefeller Foundation gifts (RF. No. 57076 and No. 54087) to that institution. The National Museum of Canada provided clerical and photographic assistance during preparation of the final manuscript. All of this aid is sincerely appreciated.

SYSTEMATIC SECTION

Class GASTROPODA

Order ARCHAEOGASTROPODA

Family FISSURELLIDAE

Genus PUNCTURELLA Lowe 1827

Type species: *Patella noachina* Linné, by monotypy.

Subgenus FISSURISEPTA Seguenza 1863

Type species: *Puncturella* (*Fissurisepta*) *papillosa* Seguenza, subsequent designation, Woodring, 1928.

PUNCTURELLA (FISSURISEPTA) AGULHASAE, new species

Plate 1, figure 3; Plate 2, figure 9

Shell small, about ⅓ inch in length, conical, base oval; fissure apical and elliptical; sculpture reticular; periostracum brown; and septum vertical. Base width about 88 per cent of the length, regularly ovate except slightly flattened anteriorly and finely crenulated by the radial ribs. Anterior and posterior slopes straight. Fissure apical, 1.0 mm. long, 0.9 mm. wide, and elliptical except flattened posteriorly where it intersects the apex of the septum. Fissure placed about 33 per cent of the distance from anterior to posterior. Sculpture reticulate, consisting of numerous, flat-topped, radiating costae and concentric cords. Costae about 50 near the apex and increasing to about 140 near the base. Intercostal spaces slightly narrower than

the costae and frequently bisected by radial threads which widen and become costae as they descend toward the base. Concentric cords about 90, not crossing the costae. Periostracum light brown, present chiefly in the intercostal spaces between the cords. Interior of shell whitish, glossy, and exhibiting the external sculpturing. Septum thin, vertical, originating at the posterior edge of the fissure, slightly convex, extending about ⅓ the distance to the base, and dividing the interior into two approximately equal halves.

	length	width	height
holotype	8.5 mm.	7.5 mm.	5.5 mm.

Types. The holotype is in the Museum of Comparative Zoology, no. 224953, from R/V VEMA station 51, Agulhas Basin about 1000 miles southwest of Capetown, South Africa, in 2507 fathoms. It was alive when collected and is the only specimen obtained.

Remarks. This species clearly belongs in *Fissurisepta* but it is apparently entirely distinct from all other species. In general shape it resembles *P.* (*F.*) *tenuicola* Dall 1927 (figured in Johnsonia, *2*, pl. 64, figs. 4-6) from 294 fathoms off Cumberland Island, Georgia, but that species is nearly smooth externally, is striated internally, and the septum is directed posteriorly. The other known species in the subgenus are more dissimilar.

Fissurisepta is primarily an archibenthal group with wide but scattered distribution in the subtropical portion of the North Atlantic, and the present species represents a sizable extension of the geographic and bathymetric range of the subgenus. For an excellent review of the genus *Puncturella* in the Western Atlantic see Johnsonia, *2*: 116-148 (1947).

Records. Known only from the type locality.

Family SEGUENZIIDAE

Genus SEGUENZIA "Jeffreys" Seguenza 1876

Type species: *Seguenzia formosa* Jeffreys, subsequent designation, Harris, 1897.

Verrill (1884) erected a separate family (Seguenziidae) for *Seguenzia* and *Basilissa* (Watson, 1879) and because of its radular characteristics placed it next to the Strombidae (Mesogastropoda). Other authors (Dall, 1889a, 1927b; Woodring, 1928; Johnson, 1934) retained the group as a family but did not agree on its relationships. Thiele (1925, 1931) placed *Seguenzia* in

the Trochidae (Archaeogastropoda) under the subfamily Margaritinae. This action was followed uncritically by Wenz (1938).

The characteristic morphology of *Seguenzia* sets these archibenthal and abyssal gastropods apart from all others. They resemble members of the archaeogastropod family Trochidae in shell shape and in the possession of nacre, but the radula approaches the typical taenioglossate type of mesogastropods, and the aperture is characterized by having one well developed posterior sinus and one or two anterior ones. The present writer therefore follows earlier authors in regarding *Seguenzia* as belonging to a separate family, the Seguenziidae. Its place in the system is questionable, but for the present, it is left next to the Trochidae following Johnson, 1934. *Basilissa* probably belongs here also.

According to Wenz (1938: 277) the oldest fossils of *Seguenzia* are from the Eocene. There are also morphological similarities between *Seguenzia* and the Ordovician to Devonian genus *Proturritella* Koken 1889 figured by Wenz (1938, fig. 436 b, c, e) and Knight (1941, pl. 39, fig. 5 a-c). Knight (personal communication) concludes that the resemblance is probably superficial.

In addition to the uncertainties regarding the systematic status and position of *Seguenzia*, difficulties often arise in defining the morphological limits of the included species. The following quotation from Dall (1889a: 269) illustrates this condition in *S. formosa* Jeffreys (= *S. monocingulata* [Seg.]).

"In examining the specimens of *Seguenzia* . . . I find myself in a dilemma. Either each separate individual is to be regarded as a species, or the variability of the shells is very great. Persistent study of the specimens has convinced me that the latter is the true solution, and that the most evident characters, such as the umbilicus (in some adult specimens) may be present or absent; that the number of spiral threads, their strength and sharpness on the basal disk, are entirely inconstant, and, while in the typical *formosa* the ridge next to the suture is waved or granulate, in many it is perfectly plain."

Similar variation is seen in other species of *Seguenzia* and minor differences probably cannot be used to separate species. It is with such a liberal attitude that the following specimens have been identified, several of which are slightly different from the type specimens or original figures with which they were compared, but sufficiently close to be considered conspecific.

Seguenzia antarctica Thiele 1925

Plate 3, figure 10

Three specimens were found which seem to fit this species, one each at station 18 (2262 fathoms, near the northern edge of the Cape Basin and approximately 400 miles west of Walvis Bay, South-West Africa), station 50 (2064 fathoms, near the southern end of the Mid-Atlantic Ridge in the Atlantic Indian Antarctic Basin), and station 53 (2670 fathoms, Cape Basin, about 300 miles southwest of Capetown, South Africa). The species is truly abyssal; the only other recorded specimen being Thiele's type collected from approximately 2520 fathoms at 63°16.5′ S, 57°51′ E in the eastern end of the Atlantic Indian Antarctic Basin.

Seguenzia eritima Verrill 1884

Plate 3, figure 6

One specimen collected at station 12 (2805 fathoms, mid-Argentine Basin, about 100 miles east-southeast of Buenos Aires) and two at station 18 (2262 fathoms, north edge of Cape Basin) seem to be nearer to *eritima* than to any other described species. *S. eritima* was recorded by Verrill from 1290 to 2033 fathoms south of Marthas Vineyard, Massachusetts. It is possible that the specimens here reported represent another, closely related species but they are too immature and worn to describe.

Seguenzia elegans Jeffreys 1876

Plate 2, figure 7; Plate 3, figure 5

Two specimens, one from station 12 (2805 fathoms, Argentine Basin) and one from station 18 (2262 fathoms, Cape Basin) agree rather closely with specimens of *elegans* in the Jeffreys Collection now in the United States National Museum (no. 181660). *S. elegans* was described from between 740 and 1095 fathoms off Portugal. The specimens also somewhat resemble *S. orientalis* Thiele 1925 from off East Africa in 379 fathoms, but are apparently closer to *elegans* than to any other species.

Seguenzia carinata Jeffreys 1876

Plate 4, figure 6

Four specimens of this species were found, three at station 14 (1703 fathoms, Cape Basin, about 400 miles northwest of Capetown, South Africa) and one at station 50 (2064 fathoms,

near the south end of the Mid-Atlantic Ridge, Atlantic Indian Antarctic Basin). The identifications here are more certain than in the case of any of the other seguenzias found. *S. carinata* has been recorded from depths ranging from 675 to 2199 fathoms at various localities in the North and South Atlantic, but apparently not previously from the basins herein reported.

Seguenzia louiseae, new species
Plate 4, figure 4

Shell small (2.4 mm. high), trochiform, strongly carinate, narrowly umbilicate, and fragile. Color white to slightly yellowish. Whorls five, with a sharp, prominent, finely undulate, peripheral carina and a second, large, slightly less angular carina between the periphery and the suture. On the upper whorls the latter carina appears to carry two parallel threads on its blade. Peripheral carina visible only on the body whorl. Basal disc with about twelve narrow additional carinae, the most prominent being the outer carina and that surrounding the umbilicus. Finer sculpturing on the spire consisting of one fine revolving thread below the suture and two to four fine revolving threads below the central carina. Fine, evenly spaced, longitudinal, sigmoid threads are also present on the top of the whorls and on the basal disc, gradually becoming finer on the latter as they approach the umbilicus. These threads parallel the lines of growth and indicate the presence of a well developed anterior and posterior sinus when the aperture is undamaged. Aperture iridescent within, subrhomboid, irregular, and expanded where it intersects the carinae. Columella slightly curved and extending in a tooth-like projection. Umbilicus deep and narrow, about one-twelfth the width of the shell. Nuclear whorl smooth, of medium size, paucispiral and slightly bulbous. Operculum thin, light yellow, and ear shaped.

	height (mm.)	width (mm.)
holotype, station 51 (dead)	2.4	2.7
paratype, " " (dead)	2.3	2.2[1]
" " " (dead)	1.7	1.7
" " " (alive)	1.6	1.6
" " " (alive)	0.8	0.9

Types. The holotype and four paratypes are from R/V VEMA biology station 51 (2507 fathoms, Agulhas Basin, about

[1] Last whorl broken away.

1450 miles southwest of Capetown, South Africa). Two additional paratypes are from station 18 (2262 fathoms, northern end of Cape Basin, about 400 miles west of Walvis Bay, South West Africa). The holotype is no. 224951 and the paratypes from station 51 are no. 224952 in the Museum of Comparative Zoology. Paratypes from station 18 are no. 4739 in the National Museum of Canada.

Remarks. In general shape, thickness, and in possession of an acute, nearly blade-like peripheral carina, *S. louiseae* more closely resembles *S. carinata* Jeffreys than any other species. The carina between the periphery and the suture is much heavier than in Jeffreys' figures of *carinata* (P.Z.S. 1885, pl. 5, figs. 3, 3a) however, and the sinuous axial threads, so prominent in *louiseae,* are absent on *carinata.* Although *louiseae* is apparently a very distinct species, it seems to be intermediate in general structure between *carinata* and the more heavily sculptured species of *Seguenzia,* e.g. *ionica* Watson and *costulifera* Schepman.

I take pleasure in naming this species for my wife, Louise R. Clarke.

Records. Known only from stations 51 and 18, cited above under 'Types'.

Family CYCLOSTREMATIDAE

Abyssogyra, new genus

Type species: *Abyssogyra vernae,* Clarke.

Shell small, planorbiform, weakly sculptured, and with a multispiral, corneous operculum. Sculpturing limited to lines of growth and two faintly developed, revolving carinae. Additional characters are those of the type species.

Abyssogyra lacks the heavy sculpturing and the beaded operculum of *Cyclostrema,* Marryat. It differs from *Circulus* Jeffreys in not being longitudinally ribbed. *Pseudomalaxis* Fischer, *Omalaxis* Deshayes, *Zalipais* Suter, *Omalogyra* Jeffreys, and the several genera erected by Bush (1897) and by Pilsbry and McGinty (1945-46) all differ in prominent characters from *Abyssogyra.*

Abbott (1950) has fixed the identity of the problematical *Cyclostrema cancellata* of Marryat, the type species of *Cyclostrema,* and this has had the effect of restricting the genus to include only the small, planorboid, heavily sculptured species with beaded opercula occurring in shallow water in the tropics.

This has left many of the deep sea species formerly placed in *Cyclostrema* without a proper genus. After a careful search of the literature, it has become clear that such is the case with *Cyclostrema normani* Dautzenberg and Fischer 1897. Since the species described below is apparently congeneric with *normani*, a new genus (i.e. *Abyssogyra*) is necessary to receive it.

Abyssogyra vemae, new species

Plate 3, figure 4

Shell minute (1.8 mm. wide), planorbiform, weakly sculptured, and white in color. Periostracum brown, thin, and present only in small patches. Whorls two, nearly circular in cross-section. Suture deep. Spire depressed, projecting only slightly above the body whorl. Aperture circular except in the parietal region where it is nearly straight and slightly thickened. Outer and inner lips thin and sharp. Umbilicus wide and extending to the nuclear whorl. Sculpture consisting of lines of growth and two low, medially located, revolving carinae, one located on the dorsal side of the whorls and one located ventrally. Two additional revolving carinae intersect the ends of the straight parietal lip: the upper one borders the suture, the lower ascends into the umbilicus. Nuclear portion bulbous, unsculptured, and consisting of one-half whorl. Operculum thin, corneous, yellowish gray, multispiral, and spirally ridged.

	major diameter	minor diameter	height
holotype	1.8 mm.	1.3 mm.	0.9 mm.

Types. The holotype was collected at station 49 (1497 fathoms, 56°43′ S, 27°41′ W, Atlantic Indian Antarctic Basin, south of Traverse Island, South Sandwich Islands). Only one specimen, a living one, was obtained. The holotype is in the Museum of Comparative Zoology, no. 224962.

Remarks. As stated above, in shell characters this species resembles a *Cyclostrema* without prominent sculpturing. It is probably closest to *Abyssogyra normani* (Dautzenberg and Fischer) but that species differs in having the aperture width approximately one-third the width of the shell and the spiral carinae very faintly developed, while in *vemae*, the aperture is approximately one-half the width of the shell and the carinae are rather well developed. It is also somewhat similar to *Homalogyra denticostata* Jeffreys 1884, except that in that species the spire is depressed below the level of the body whorl

and the concentric sculpturing is slightly sigmoid and more prominent.

Records. Known only from the type locality.

Genus Brookula Iredale 1912

Type species: *Brookula stibarochila* Iredale 1912, original designation.

Through the kindness of Dr. Donald F. McMichael of the Australian Museum, Sydney, and Dr. Harald A. Rehder of the United States National Museum, I have been able to examine the holotypes of *Brookula stibarochila* Iredale 1912 (Pl. 1, fig. 5) and *Vetulonia galapagana* Dall 1913 (Pl. 1, fig. 1), the type species of the genera *Brookula* and *Vetulonia,* respectively.

The anatomy and radular characteristics of these two species are unknown, but examination of the shells has led to the conclusion that their relationships are sufficiently distant to make it desirable to place them in different subgenera. *B. stibarochila,* a shallow water tropical species, is minute, umbilicate, covered with axial ribs which are approximately vertical, has a beaded aperture which is nearly parallel with the columella, and has a white, glass-like shell. *Vetulonia galapagana,* an abyssal species, is much larger, non-umbilicate (the umbilicus is neatly filled with a callus), covered with oblique axial ribs, has a plain, oblique (prosocline) aperture and a white, somewhat chalky shell.

In addition, many of the archibenthal and abyssal species formerly placed in *Brookula* appear to belong to a third group distinct from *Brookula* (*sensu stricto*) and from *Vetulonia.* This group is described below as a new subgenus and is given the name *Benthobrookula.*

Benthobrookula, new subgenus

Type species: *Brookula* (*Benthobrookula*) *exquisita* Clarke, original designation.

Shells small, umbilicate, sculptured with axial ribs which are approximately vertical and with spiral threads or costae, with a plain, nearly vertical aperture, a relatively large and slightly bulbous protoconch, and with a white, opaque, solid shell.

Benthobrookula differs from *Brookula* (*sensu stricto*) in the following characters. *Benthobrookula* has a somewhat bulbous

and relatively large protoconch; the aperture is plain, i.e. not beaded or otherwise sculptured although it may be thickened; the costae are narrow and symmetrical in cross-section; and the shell is not glassy and not translucent. *Brookula* (*sensu stricto*) has a small protoconch; the aperture is beaded; the costae are flattened, rounded in front and blade-like behind; and the shell is glassy and translucent and appears like a tropical species which, of course, it is. In operculum characteristics, the two subgenera are very similar.

From *Vetulonia, Benthobrookula* differs as follows. *Vetulonia* has the umbilicus neatly filled with a callus, the ribs are oblique, and the aperture is strongly prosocline. *Benthobrookula* is openly umbilicate and the ribs and the aperture are approximately vertical. Anatomical studies are necessary in all three of these groups, and the results of such studies may support or confound the division here proposed.

Thiele (1925: 57, 71) pointed out that much confusion existed in the proper placement of the small shells previously assigned to *Cyclostrema* (e.g. *Brookula, Vitrinella,* etc.) and proposed three groups to include them: (1) Skeneidae in which the radula has 4 or 5 lateral teeth, (2) Cyclostrematidae which has only one lateral tooth and a few weak marginal teeth, and (3) Vitrinellidae which is taenioglossate. The radula of *Brookula powelli,* n. sp. (Pl. 4, fig. 9) most clearly fits the Cyclostrematidae, notwithstanding possible differences in interpretation concerning which are lateral and which are marginal teeth.

Brookula (Benthobrookula) powelli, new species

Plate 3, figure 7; Plate 4, figures 1 and 9

Shell minute (2.3 mm. wide), trochiform, depressed, umbilicate, prominently sculptured, and grayish white. Whorls 2⅝, convex, separated by a depressed suture and forming a slightly obtuse spire. Sculpture consisting of numerous, rather heavy, narrow, longitudinal ribs (40 on the body whorl and 32 on the penultimate whorl of the holotype) and numerous, very fine revolving threads (about 30 on the body whorl of the holotype) which do not cross the ribs. The threads become somewhat stronger on the base of the shell, but except for the four cords which surround the umbilicus, the spiral striations never approach the ribs in strength. The four cords around the umbilicus are of approximately the same strength as the ribs. Aperture complete, ovate, somewhat angled posteriorly

and flattened where it is appressed to the preceding whorl. Outer and inner lips slightly thickened. Umbilicus rather wide and extending far up into the shell. Periostracum apparently absent. Protoconch bulbous, smooth, and composed of one-half whorl. Operculum thin, round, corneous, multispiral, and yellowish. Radula (from a station 51 specimen) shown in Plate 4, figure 9.

	height (mm.)	width (mm.)	whorls
holotype, station 12	1.9	2.3	2⅝
paratype, station 51	1.6	2.0	2⅞
paratype, station 51	1.5	1.7	2⅝
paratype, station 51	1.3	1.4	2¾

Types. The holotype containing the animal is from R/V VEMA biology station 12 (2805 fathoms, mid-Argentine Basin, about 1000 miles east-southeast of Buenos Aires, Argentina). One paratype, living when collected, is from station 48 (1902 fathoms, about 100 miles southeast of South Georgia) and thirteen paratypes, most of which contain the animal, are from station 51 (2507 fathoms, about 1000 miles southwest of the Cape of Good Hope). The holotype is no. 224960 in the Museum of Comparative Zoology. Paratypes are in the Museum of Comparative Zoology and the National Museum of Canada.

Remarks. Brookula (*Benthobrookula*) *powelli* is similar to *Brookula strebeli* and *B. pfefferi* (both Powell, 1951, from off South Georgia in 85 to 97 fathoms) in general appearance and in the possession of umbilical cords, but those species are higher than wide and exhibit 3½ and 4¾ whorls, respectively, although they are both smaller than the holotype of *powelli* which has only 2⅝ whorls. In addition, the axial sculpturing and the spiral threads are finer on *powelli*.

The species is named for Dr. A. W. B. Powell of the Auckland Museum, who has been for many years the leading authority on Antarctic mollusks.

Records. Known only from the localities cited above under 'Types'.

Brookula (Benthobrookula) exquisita, new species

Plate 3, figure 8; Plate 4, figure 2

Shell minute (1.8 mm. wide), trochiform, depressed, umbilicate, heavily sculptured, and white. Whorls 2¾, convex, separated by a depressed suture and forming a spire which is

produced at an angle of about 120°. Sculpture consisting of numerous rather heavy, narrow, longitudinal ribs (28 on the body whorl and 23 on the penultimate whorl of the holotype) and many prominent revolving cords (17 on the body whorl of the holotype), which give the shell a cancellated appearance. The cords on the top of the whorls are weaker than the ribs, but on the base, except for the three major cords surrounding the umbilicus, the cords and ribs are of approximately the same strength. The three cords near the umbilicus are more widely spaced and are much heavier than the ribs. Aperture circular except slightly flattened where it is appressed to the preceding whorl and lightly crenulated by the three major basal cords. Outer lip somewhat thickened, inner lip a little thinner. Umbilicus deep, wide at the base and narrowing as it ascends. Periostracum apparently absent. Nuclear portion bulbous, smooth, and composed of one-half whorl. Operculum thin, round, corneous, multispiral, and yellowish.

	height (mm.)	width (mm.)	whorls
holotype, station 47	1.5	1.8	2¾
paratype, station 47	1.2	1.4	2⅝

Types. The holotype and one paratype, both living specimens, were dredged at R/V VEMA Biology Station 47 (2054 fathoms, approximately 60 miles south of South Georgia). The holotype is no. 225954 in the Museum of Comparative Zoology and the paratype is no. 4742 in the National Museum of Canada.

Remarks. This species more closely resembles *B. powelli* than any other species, but the spiral cords are very much heavier in *exquisita* and the spire is markedly more obtuse. *B. pfefferi* Powell (1951) and *B. strebeli* Powell (*loc. cit.*) are somewhat similar also, but in those species the spire is acute and the spiral threads are very weak, nothing like the robust thickness of the threads in this species.

Records. Known only from the type locality.

Brookula (Benthobrookula) lamonti, new species

Plate 4, figure 3

Shell minute (1.5 mm. wide), trochiform, not depressed, sculptured, umbilicate, and white. Whorls 3¼, convex, separated by a sharply defined, depressed suture and forming a slightly acute spire. Sculpture consisting of numerous, sharp, somewhat elevated longitudinal ribs (25 on the body whorl and 22 on

the penultimate whorl of the holotype) and many fine, low, revolving threads (about 20 in the holotype) which do not cross the ribs. The threads become a little stronger on the base of the shell, but except for the two threads which border the umbilicus, they are much weaker than the ribs. The two cords near the umbilicus are about the same strength as the ribs. Aperture ovate-ear shaped, angled posteriorly and flattened where it is appressed to the preceding whorl. Outer and inner lips thickened. Umbilicus rather narrow and deep. Periostracum apparently absent. Nuclear portion partly broken in the holotype but apparently bulbous, smooth, and composed on one-half whorl. Operculum thin, round, corneous, multispiral, and yellowish.

	height (mm.)	width (mm.)	whorls
holotype, station 47	1.5	1.4	3¼

Types. The holotype, an unique specimen, was collected alive at R/V VEMA biology station 47 (2054 fathoms, Scotia Sea about 60 miles south of South Georgia). It is at the Museum of Comparative Zoology, no. 225953.

Remarks. This species is grossly similar to *B. pfefferi* Powell (1951) and *B. strebeli* Powell (*loc. cit.*) (which are so similar to each other that they appear to represent the same species), but *lamonti* has a much thicker lip than either of those species, the aperture is angular posteriorly while in *pfefferi* and *strebeli* it is not, and the umbilical area in *lamonti* is more open and quite differently sculptured. From *powelli* and *exquisita,* described above, *lamonti* may be differentiated by its slightly acute spire, its heavier lip, its less prominent ribs, and its more chalky appearance.

This species is named for the Lamont Geological Observatory, the sponsor of the expeditions which led to the discovery of the mollusks here described.

Records. Only one specimen is known. See under 'Types'.

Brookula (Benthobrookula) capensis, new species

Plate 1, figure 4

Shell small (3.4 mm. wide), trochiform, not depressed, heavily sculptured, white on the ribs and light brown between them. Spire turreted and acute. Whorls approximately 3 to 4 (nuclear portion broken away), convex, and separated by a deep suture. Sculpture consisting of numerous, elevated, slightly sigmoid

longitudinal ribs (26 on the body whorl and 20 on the penultimate whorl of the holotype) with one to three low longitudinal threads in the spaces between the ribs. Numerous fine spiral threads are also present (about 35 on the body whorl in the holotype) extending all over the whorls and up into the umbilicus. The threads on the base are a little heavier, but no prominent cords surround the umbilicus. Aperture ovate, slightly angular posteriorly, and in contact with the preceding whorl only in a narrow zone. Lip thickened anteriorly and only slightly thickened elsewhere. Umbilicus narrow and deep. Periostracum thin, light brown. Nuclear whorls not visible. Operculum thin, round, corneous, multispiral, light brown generally with a yellowish-green central area.

	height (mm.)	width (mm.)	visible whorls
holotype	3.2[1]	3.0	2½

Types. The holotype, an unique specimen, was collected alive at R/V VEMA biology station 53 (2670 fathoms, Cape Basin, about 300 miles southwest of Capetown, South Africa). It is in the Museum of Comparative Zoology, no. 225952.

Remarks. With respect to lacking umbilical carinae, this species is similar to *B. valdiviae* Thiele 1925, *B. kerguelensis* Thiele 1925, *B. decussata* (Pelseneer) 1903, *B. conica* (Watson) 1886, *B. crassicostata* (Strebel) 1908, *B. calypso* (Melville and Standen) 1912, and *B. cancellata* (Jeffreys) 1883. However, in addition to being larger than any of these, the following differences may be seen.

The spire of *capensis* is acute while that of *crassicostata* and *cancellata* is obtuse. In *capensis* the ribs are sigmoid and the spiral striae cross the ribs, while in *valdiviae, kerguelensis, conica,* and *decussata* the ribs are straight and the spiral striae do not cross them. *B. calypso* differs in having straight ribs and two prominent lines around the penultimate whorl.

Records. Known only from the type specimen. See 'Types'.

Family CHORISTIDAE

Genus CHORISTES Carpenter 1872

Type species: *C. elegans* Carpenter 1872, by monotypy.

The genus *Choristes* was proposed by Carpenter (in Dawson, 1872) to receive the post-Pliocene species *C. elegans* Carpenter.

[1] Upper whorl(s) broken away.

Verrill (1882) described a living species from 255 fathoms off Marthas Vineyard which he considered only as a variety of *elegans,* viz. *C. elegans* var. *tenera.* Bush (1897), working with additional material from off Marthas Vineyard, compared the radula of a similar species from 390 fathoms with *tenera.* She found that the "new" species possessed two single overlapping lateral teeth (Bush, 1897, pl. 23, fig. 16) in the position occupied, in *tenera,* by the single, wide, bilobed second lateral (Verrill 1882, pl. 58, fig. 27a) and that there were consequently thirteen teeth in each transverse row in the new species instead of eleven, the number in *tenera.* Bush therefore created the new genus *Choristella* to receive this new species (*leptalea*) and another species (*brychia*) represented by a single dead specimen dredged off Marthas Vineyard in 810 fathoms and described in the same paper.

Examination of the type specimens of the above species from the collections of the United States National Museum has resulted in the following conclusions. In shell characters *tenera* and *elegans* are very similar except that the shell of *tenera* is much thinner than that of *elegans,* as was pointed out by Verrill (*loc. cit.*) In view of this constant and striking difference and the fact that *elegans* is post-Pliocene and existed in shallow water while *tenera* is recent and archibenthal, the two forms are here considered as separate species.

On the other hand, the type specimens of *leptalea* and *brychia,* although not equally corroded, are apparently identical to each other and to *tenera.* The type localities of the three species are all in the same general area on the continental slope south of New England. In view of these factors, the writer considers that the differences in the radulae which have been illustrated (*loc. cit.*) may be due to different interpretations by the two authors as to whether the second lateral was actually a single, wide tooth with two cusps, or two separate, overlapping teeth each with a single cusp, and that both authors probably observed radulae of the same species.

It is, therefore, considered that the family Choristidae contains only the genus *Choristes,* with *Choristella* as a synonym. After the addition of two species described by Dall (not discussed above) the list of species in *Choristes* is as follows: *elegans* Carpenter 1872, *tenera* Verrill 1882, *carpenteri* Dall 1896, *pompholyx* (Dall) 1889, *agulhasae* (*sensu stricto*) and *agulhasae argentinae,* a new species and a new subspecies to be described below.

Choristes agulhasae, new species

Plate 3, figure 1

Shell small (3.0 mm. wide), somewhat depressed, moderately sculptured, umbilicate, semi-transparent, and very fragile. Whorls three, convex, separated by an incised suture, and forming a flattened, obtuse spire. Color grayish white except on the body whorl where the shell becomes transparent and longitudinal streaks of white appear. Sculpture consisting of fine lines parallel to the lines of growth; a low, centrally located, basal carina; a second carina running up inside the umbilicus; and a low carina on the upper part of the whorl near the suture. The latter carina becomes obsolete on the body whorl. Aperture large, ovate, and flattened at the inner edge. Inner lip nearly straight, oblique, and thin. Outer lip thin and convex. Umbilicus rather wide and extending to the protoconch. Protoconch small, planospiral, and consisting of about ½ whorl. Operculum diaphanous, transparent, and apparently paucispiral.

	height (mm.)	width (mm.)	whorls
holotype	2.0	3.0	3

Types. The holotype, an unique specimen, was collected alive and unbroken at R/V VEMA biology station 51 (2507 fathoms, Agulhas Basin, approximately 1000 miles southwest of Capetown, South Africa). It is in the Museum of Comparative Zoology, no. 224955.

Remarks. This species, the first in this genus to be recorded from the Southern Hemisphere, is readily distinguished from all other species of *Choristes* by its rather strong basal carinae and long, straight parietal lip. (For differential characters between this and the following subspecies *C. a. argentinae,* see *Remarks* under *argentinae.*) The other species all lack the carinae and exhibit a curved parietal lip. In addition, *pompholyx* Dall is thicker, white, and polished, while *elegans* Carpenter and *tenera* Verrill appear to be much larger species, although, of course, we do not know what the maximum size of *agulhasae* may be.

Records. The holotype is the only known specimen. See under 'Types'.

Choristes agulhasae argentinae, new subspecies

Plate 3, figures 2 and 3

Shell small (3.5 mm. wide), somewhat depressed, loosely coiled, moderately sculptured, umbilicate, heavily eroded, and rather fragile. Apex decollated, leaving only 1⅔ whorls. Color

light yellowish brown except white where the outer layer of the shell has been corroded away. Whorls convex, enlarging rapidly, separated by a narrow incised suture, and touching only in a narrow peripheral zone. Sculpture visible only in uncorroded areas and consisting of fine, incremental lines parallel to the lines of growth. There is a single, prominent, centrally located carina on the base of the body whorl and another carina, scarcely visible in the holotype because of corrosion, but apparently revolving up inside the umbilicus. Aperture large and obliquely D-shaped. Inner lip straight, oblique and slightly thickened. Outer lip rather thin and convex. Umbilicus rather wide, extending through the shell, and exposed apically. Protoconch and operculum not present.

	height (mm.)	width (mm.)	whorls
holotype	2.3	3.5	1⅔

Types. The holotype, without the animal and an unique specimen, was collected from R/V VEMA biology station 12 (2805 fathoms, mid-Argentine Basin, approximately 1000 miles east-southeast of Buenos Aires, Argentina). It is in the Museum of Comparative Zoology, no. 224956.

Remarks. This subspecies is similar to *C. agulhasae* (*sensu stricto*) except for the following characters. *C. a. argentinae,* where it is not corroded, exhibits a somewhat thickened, semi-translucent shell with a yellowish periostracum while in *C. agulhasae* the shell is uniformly thin (much thinner than *argentinae*), transparent on the body whorl, and without any visible periostracum. In addition, the uncorroded portions of *argentinae* indicate that the region of the body whorl adjacent to the suture is slightly concave, a characteristic not seen in *agulhasae.* Finally, the aperture in *argentinae* is more expanded and the parietal lip is straighter, longer, and much thicker than in *agulhasae.*

Records. Known only from the type locality. See under 'Types'.

Order MESOGASTROPODA

Family NATICIDAE

Genus AMAUROPSIS Mörch 1857

Type species: *Natica helicoides* Johnston 1835, subsequent designation, Dall 1909.

Subgenus KERGUELENATICA Powell 1951

Type species: *A.* (*K.*) *grisea* (von Martens) 1878, original designation, Powell 1951.

AMAUROPSIS (KERGUELENATICA) GRISEA (von Martens) 1878

Plate 1, figure 6

One dead specimen which appears to be this species was trawled at R/V VEMA station 14 (1703 fathoms, Cape Basin, about 400 miles northwest of Capetown, South Africa). It was inhabited by a pale, blind, abyssal hermit crab. Another specimen, living when collected, which unquestionably belongs to *grisea,* was trawled at station 51 (2507 fathoms, Agulhas Basin, about 1000 miles southwest of Capetown, South Africa). This exhibited the characteristic operculum which is horny with a prominent, thin calcareous layer over the central part, and was otherwise identical to the published figures of *grisea.* A third specimen, which is probably this species, was trawled, also alive, at station 47 (2054 fathoms, Scotia Sea, about 60 miles south of South Georgia). It too is very similar to the published figures of *grisea* but the operculum has a heavier calcareous layer than in typical *grisea* and it covers the entire outer surface.

About six other naticoid species are present in the R/V VEMA material from stations 46, 47, 49, and 51 (1497 to 2507 fathoms, Scotia Sea and Agulhas Basin), but without type material for comparison I do not wish to name them at this time. They appear to belong to the group characterized by Hedley (1916) as follows: "There is an Antarctic naticoid group which . . . amounts to about a dozen rather featureless species, all small, mostly uniform olive buff in color, four whorls, a slightly raised spire, a caducous epidermis, comparatively thin, unsculptured, except for incremental striae, without umbilical funicle or a callus pad at the insertion of the right lip. Operculum corneous paucispiral." Since the VEMA stations are in general much deeper than any other stations in the sub-Antarctic from which mollusks have been reported, identifications of these species with previously described species would appear to constitute large extensions of their bathymetric ranges, and such extensions might be incorrect.

Order NEOGASTROPODA

Family BUCCINULIDAE[1]

Genus TROMINA Dall 1918

Type species: *Fusus unicarinatus* Philippi, original designation.

TROMINA BELLA ABYSSICOLA, new subspecies

Plate 2, figure 10; Plate 4, figure 7

Shell small (11.8 mm. long) buccinoid, moderately sculptured, and thin. Whorls 3⅔, convex, separated by a rather deep suture, and forming a spire which subtends an angle of about 70°. Sculpturing consists of numerous, narrow, low, closely spaced spiral ribs (about 45 on the body whorl of the holotype) and numerous unevenly spaced axial ribs (about 75 on the body whorl of the holotype) similar to the spiral ribs in height and thickness, which give the surface a reticulated appearance. Aperture rather large and with a wide siphonal canal, smooth and shiny within and there exhibiting the external sculpture. Columella twisted. Parietal wall convex anteriorly and posteriorly, concave medially with a straight central portion, and with a thin callus over its whole surface. Outer lip thin, sharp, broadly convex, and crenulated by the spiral ribs. Umbilicus absent. Periostracum rather thin but prominent and yellowish brown. Nuclear whorls 1¾, forming a dome-shaped protoconch sculptured with fine, slightly wavy, longitudinal ribs and nearly imperceptible spiral lines. Operculum thin, filling about half the aperture, light yellowish, paucispiral, and with the nucleus sub-terminal. Radula with a tricuspid central tooth and bicuspid marginals (Pl. 4, fig. 7).

	height (mm.)	width (mm.)	whorls
holotype, station 51	11.8	7.5	3¾
paratype, station 51	7.2	4.9	3½

Types. The holotype and one paratype, the only specimens known, were collected alive at R/V VEMA biology station 51 (2507 fathoms, Agulhas Basin, about 1000 miles southwest of Capetown, South Africa). The holotype is in the Museum of Comparative Zoology, no. 224954. The paratype is in the National Museum of Canada, no. 4739.

[1] The writer is following Powell (1951) in the use of this family name.

Remarks. *T. bella abyssicola* is similar to *T. bella* Powell 1951 (82-152 fathoms, from four localities near the Falkland Islands) in most of its characters and is apparently closely related to it. The observed differences seem to be entirely sufficient to justify its subspecific status however, especially in view of the great divergence in depth and the great distance between the localities.

T. b. abyssicola is a much thinner and more delicate species than *T. bella.* The external sculpturing shows clearly inside the aperture in *abyssicola* but does not show in *bella.* The parietal wall in *abyssicola* has a straight portion in the center while in *bella* the central region is rather evenly concave. In addition, the central tooth of the radula of *abyssicola* bears a larger central and two markedly smaller lateral cusps and the two cusps of each marginal are of approximately equal size (Pl. 4, fig. 7). In *bella* however, the central tooth bears three cusps of the same size and the inner cusp of the marginals is larger than the outer (Powell 1951, p. 194, fig. 72). The shape of the teeth is also somewhat different in the two subspecies.

The shell of this subspecies is very similar to some species in the taenioglossate archibenthal and abyssal genus *Oocorys* (family Tonnidae, see Turner, 1948) and represents another case of parallel evolution among unrelated groups. Certain of the published records of *Oocorys* from southern high latitudes may well be based on species of *Tromina.*

Records. Known only from the type locality. See under 'Types'.

Tromina traverseensis, new species

Plate 2, figure 8

Shell small (6.6 mm. long), buccinoid, weakly sculptured, and thin. Whorls 3⅔, convex, shouldered, separated by a deep suture and forming a spire which subtends an angle of about 80°. Sculpture consisting of many narrow, low, rounded spiral ribs (about 43 on the body whorl of the holotype) which appear as whitish lines on a pale buff background, crossed by very fine, crowded lines of growth. Aperture large (about ⅔ the length of the shell), with numerous narrow, shallow grooves within, resulting from the external ribbing, and with a wide siphonal canal. Columella twisted. Parietal wall convex anteriorly and posteriorly and concave centrally and glazed with a thin callus which does not obscure the sculpturing beneath.

Outer lip thin, sharp, broadly convex and lightly crenulated by the spiral sculpture. Umbilicus small and nearly closed by the flexion of the parietal callus. Periostracum thin, yellowish brown, and occurring mainly between the spiral ribs. Nuclear whorls 1½, nearly smooth, and forming a dome shaped protoconch. The holotype, containing the soft parts, has no operculum.

	height (mm.)	width (mm.)	whorls
holotype, station 49	6.6	4.5	3⅔
paratype, station 49	2.7	2.0	2¼

Types. The holotype and paratype, respectively with and without the soft parts, were collected at R/V VEMA biology station 49 (1497 fathoms, south of Traverse Island, South Sandwich Islands). The holotype is in the Museum of Comparative Zoology, no. 224963. The paratype is in the National Museum of Canada, no. 4738.

Remarks. T. traverseensis is somewhat similar to *T. simplex* Powell 1951 in sculpturing, but *traverseensis* has strongly convex, shouldered whorls, an umbilicus, is very thin, and shows the external sculpturing within the aperture, while *simplex* has only lightly convex, unshouldered whorls, lacks an umbilicus, is substantially thicker, and does not exhibit the internal sculpturing within the aperture. Compared with *T. bella abyssicola* Clarke, *traverseensis* has much finer sculpturing and possesses an umbilicus while *abyssicola* does not.

Records. The only known specimens are the holotype and paratype. See under 'Types'.

Shells of what now appear to be three additional new species of *Tromina* (or possibly *Notoficula* Thiele 1917) are in the R/V VEMA material. Each is represented by a single specimen, of which two are somewhat broken empty shells and probably immature (from VEMA stations 47 and 53) and one is very young and contains the soft parts (station 47). So little is known of the degree of variation to be expected among these Antarctic whelks that it is quite uncertain whether these will prove to be outside the range of variation of known species or not. If they are similar to northern whelks in this regard (*Buccinum*, *Neptunea*, *Colus*, etc.), much variation may be expected. For this reason, I do not wish to describe them until more material is available and in further discussions will refer to them simply as *Tromina* a, b, and c, respectively.

Class PELECYPODA

Order PROTOBRANCHIATA

Family NUCULIDAE

Genus NUCULA Lamarck 1799

Type species: *Arca nucleus* Linné, by monotypy.

NUCULA TURNERAE, new species

Plate 2, figures 2 and 3

Shell minute (1.8 mm. long), ovate, sub-inflated, nearly smooth, thin and with a broadly curved hinge plate bearing few teeth. Valves fragile and semi-transparent. Outline ovate except for the protruding umbones (which are placed about 36 per cent of the length from the posterior end), a slightly pointed anterior end (the longer end), and a somewhat flattened posterior end. Sculpture consisting of numerous fine lines of growth and microscopic radial lines. Larval valves very small, caplike and covering only the dorsal part of the umbones. Periostracum very thin and pale brown. Inner surface shiny, exhibiting well-marked muscle scars and a simple pallial line. Shell margin smooth and covered by periostracum. Hinge plate broadly curved, narrowed anterior to the chondrophore. Anterior row with three and posterior row with two, medium-sized, pyramidal, dorso-ventrally compressed taxodont teeth. Hinge plate expanded at the chondrophore which is small, triangular-ovate, and directed obliquely anteriorly. Umbones excavated.

	length (mm.)	height (mm.)	width (mm.)
holotype, station 12	1.8	1.5	1.0

Types. The holotype, an unique specimen, was collected alive at R/V VEMA biology station 12 (2805 fathoms, Argentine Basin, about 1000 miles east-southeast of Buenos Aires, Argentina). It is in the Museum of Comparative Zoology, no. 224959.

Remarks. The simple, plain and fragile shell of *turnerae* renders it distinct from all other abyssal nuculas from the South Atlantic Ocean. In general appearance it approaches *N. pernambucensis* Smith 1885 from off Recife, Brazil, in 675 fathoms (CHALLENGER, sta. 120), but that species is larger, much more quadrate and bears about eleven teeth in each valve while *turnerae* bears only five. It is possible that *turnerae* is immature, but the thin, fragile, nearly unsculptured shell is

typical of deep abyssal species and the tiny attached larval shell suggests that the holotype is probably adult or nearly so.

This species is named in honor of Dr. Ruth D. Turner who has generously aided the writer in numerous matters connected with this work.

Records. The holotype is the only known specimen. See under 'Types'.

Genus PRONUCULA Hedley 1902

Type species: *Pronucula decorosa* Hedley 1912, original designation.

PRONUCULA BENGUELANA, new species

Plate 3, figures 9 and 11

Shell nuculiform, slightly inflated, small (about 3.5 mm. long), radially sculptured, thin and with a curved hinge plate. Valves semi-transparent and showing the teeth, intestine, etc. through the shell. Outline triangular-ovate, rounded and slightly pointed posteriorly, broadly curved ventrally, more abruptly curved anteriorly (sometimes slightly pointed) and with prominent, inflated umbones placed about 40 per cent of the length from the posterior end. Adult sculpture consists of numerous (about 65 to 75) narrow, rounded radial ribs over the whole central area crossed by crowded, microscopic lines of growth. Larval shells white, persistent, large (about 30 per cent of the height of the adult) and sculptured with fine concentric lines and microscopic radial lines. Periostracum thin, lustrous and light yellowish brown. Inner surface nacreous and exhibiting the external radial ribs. Muscle scars and simple pallial line well marked. Shell margin smooth, not crenulated. Hinge plate nearly straight posteriorly, rather sharply curved centrally and broadly curved anteriorly. Posterior row with six and anterior row with nine columnar, pointed, slightly curved teeth. Chondrophore small, triangular, approximately vertical and close to the innermost taxodont teeth. Umbones deeply excavated.

	length (mm.)	height (mm.)	width (mm.)
holotype, station 14	3.8	3.4	2.0
paratype, station 14	3.3	3.0	1.8
paratype, station 14	3.2	2.9	1.8
paratype, station 14	2.9	2.4	1.6

Types. The holotype and 26 paratypes, all living specimens, plus a single valve, were collected at R/V VEMA station 14 (1703 fathoms, Cape Basin, about 400 miles northwest of Capetown, South Africa). The holotype is in the Museum of Comparative Zoology, no. 224964. Paratypes are in the Museum of Comparative Zoology and the National Museum of Canada.

Remarks. Pronucula benguelana is one of a widespread deep sea complex which includes *P. notobenthalis* (Thiele) 1912 from 1490 fathoms from the western end of the Eastern Indian Antarctic Basin and *P. profundorum* (Smith) 1885 from 2050 fathoms from the mid-North Pacific. It differs from *profundorum* in that *profundorum* is much more pointed posteriorly and the beaks are more centrally located. Conversely, from *notobenthalis* it differs in that the posterior extremity is much more rounded and the beaks are located more anteriorly in that species; also *notobenthalis* is much more oblique.

The name *benguelana* refers to the type locality, which is beneath the region traversed by the Benguela Current.

Records. In addition to the holotype and paratypes, there are thirteen specimens from station 47 (2054 fathoms, Scotia Sea, about 60 miles south of South Georgia) which are doubtfully referred to this species. They are very similar to the specimens from the type locality except that the larval shells are proportionately larger and the adult outline is more broadly curved posteriorly. Such differences may be expected between isolated populations of abyssal mollusks because of very restricted gene flow between them. In this case the differences are relatively minor and I prefer not to designate this population as a distinct subspecies.

Family MALLETIIDAE

Genus MALLETIA Desmoulins 1832

Type species: *Malletia chilensis* Desmoulins, by monotypy.

MALLETIA PALLIDA Smith 1885

This species was taken at R/V VEMA biology station 47 and 52 (2054 fathoms, Scotia Sea, approximately 60 miles south of South Georgia; and 2711 fathoms, Agulhas Basin, approximately 800 miles southwest of Capetown, South Africa, respectively). A series of 15 specimens was collected at station 52, with individuals ranging from 3.0 to 19.5 mm. in length.

The larger specimens are identical to the figures in Smith (1885, pl. 20, figs. 8, 8a). The smaller specimens are very similar to the three small specimens from station 47, which otherwise would not have been recognized as belonging to *pallida*. The type locality is CHALLENGER station 137, 2550 fathoms, 35°59′ S., 1°34′ E., in the Cape Basin, not far from VEMA station 52.

Malletia johnsoni, new species
Plate 2, figure 6

Shell small (about 6 mm. long), rectangularly ovate, compressed, nearly smooth, very thin and fragile, and with a narrow, weak and almost straight hinge plate. Valves somewhat translucent, thin and brittle. Dorsal margin nearly straight; anterior margin rounded and curving smoothly to the ventral margin which is less sharply rounded; posterior broader than anterior and truncated. Umbones rather small, placed a little in front of center. Sculpture consisting only of fine lines of growth. Periostracum thin, shiny, and pale yellowish brown. Ligament extending from slightly in front of the beaks to near the posterior margin. Inner surface white, only slightly lustrous and with muscle scars and a relatively large pallial sinus located above the midline of the valves. Shell margin finely crenulated. Hinge plate narrow, nearly straight, a little bent down anteriorly, wider distally than centrally, and bearing about 7 anterior and 10 posterior small V-shaped taxodont teeth. Teeth larger distally and becoming obsolete and vanishing near the beaks. Umbones not excavated.

	length (mm.)	height (mm.)	width (mm.)
holotype, station 22	4.7	3.1	1.4
paratype, station 22	6.2	3.8	1.6
paratype, station 22	4.0	2.5	1.2

Types. The holotype and six paratypes were collected alive at R/V VEMA biology station 22 (1675 fathoms, Angola Basin, about 175 miles west of Banana, Belgian Congo). The holotype is in the Museum of Comparative Zoology, no. 224961. Paratypes are in the National Museum of Canada, no. 4737.

Remarks. Malletia johnsoni is characterized by its small size, its compressed, thin, and fragile valves, and its broad, truncate posterior end. It resembles the North Atlantic *M. obtusata* Sars in general, but that species is not broader posteriorly, the

beaks are farther forward and the valves are not convex. *M. dilatata* Philippi is much more heavily sculptured and the posterior end is more sharply truncated. *M. johnsoni* is not similar to any South Atlantic species.

This species is named in honor of Richard I. Johnson, who for many years has been a most enthusiastic and careful worker in malacology.

Records. In addition to the type lot, two specimens which probably belong to this species were collected at station 54 (993 fathoms, Cape Basin, about 65 miles northwest of Capetown, South Africa). They are very similar to the types except that the valves are a little larger (7.0 mm. long) and significantly more transparent. Seen through the shell, the number of teeth also appears to be a little greater, but this is no doubt because of the greater length.

Malletia concentrica Thiele 1912

Ten specimens of one species of *Malletia* ranging in length from 2.0 to 5.3 mm. were taken at R/V VEMA biology station 49 (1497 fathoms, Atlantic Indian Antarctic Basin, south of Traverse Island, South Sandwich Islands) and three other specimens ranging from 1.5 to 2.7 mm. in length were taken at station 16 (1660 fathoms, Cape Basin, approximately 175 miles west-northwest of Lüderitz, South-West Africa). The smaller specimens resemble Thiele's figures (1912: pl. 17, figs. 24, 24a) of *concentrica* very closely (the holotype is 2.75 mm. long) and probably belong to that species. The type locality of *concentrica* is 1872 fathoms northeast of Gauss Station in the western end of the Eastern Indian Antarctic Basin. Larger specimens of *concentrica* from station 49 are expanded post-basally and are quite unsymmetrical in shape. The species is markedly convex, the largest specimen measuring 5.3 mm. in length, 3.8 mm. in height and 2.8 mm. in width.

Genus Tindaria Bellardi 1875

Type species: *Tindaria arata* Bellardi, by monotypy.

Tindaria virens Dall 1890

At R/V VEMA biology station 22 (1675 fathoms, Congo Canyon, Angola Basin, about 175 miles west of Banana, Belgian Congo) twelve living specimens were collected which agree closely with paratypes of *Tindaria virens* Dall. The only

observable difference is that the hinge teeth are a little heavier in the VEMA specimens than in *virens*, but this difference is probably too slight to be given taxonomic significance. *T. virens* was taken by Dall off southern Chile in 122 to 449 fathoms.

Tindaria championi, new species
Plate 2, figures 1 and 4

Shell small (5.8 mm. long), veneriform, sub-inflated, moderately strong, rather weakly sculptured and with an angular hinge plate bearing taxodont hinge teeth. Outline oval except for the prominent beaks which are placed about 40 per cent of the way from the anterior end. Sculpture consisting of numerous narrow, very low, rounded concentric ribs, fine near the umbones and becoming coarser near the ventral margin, and crowded, exceedingly fine radial lines. Periostraeum thin, light brown and beautifully iridescent. Ligament narrow, about 18 per cent the length of the shell, and extending posteriorly from under the umbones. Inner surface white, sub-nacreous, with prominent muscle scars, pallial line and pallial sinus. Shell margin smooth. Hinge plate strong, bent and a little narrowed under the umbones and bearing seven anterior and nine posterior, erect, V-shaped, conical taxodont teeth. Teeth much higher in the center of each row, becoming obsolete near the umbones, and not meeting under the umbones. Umbones excavated.

	length (mm.)	height (mm.)	width (mm.)
holotype, station 12	5.8	4.8	2.8

Types. The holotype was taken alive at R/V VEMA biology station 12 (2805 fathoms, Argentine Basin, about 1000 miles east-southeast of Buenos Aires, Argentina). It is in the Museum of Comparative Zoology, no. 224957.

Remarks. Tindaria championi is another species of the veneriform, concentrically sculptured group in *Tindaria* which has a prominent pallial sinus (see *T. crebus* Clarke 1959b). *T. championi* may be distinguished from *T. crebus* by the much heavier sculpture, many more teeth, regularly curved central portion of the hinge plate, and larger size of *crebus*. It differs from *T. antarctica* Thiele and Jaeckel in shape (subrectangular in *antarctica* and oval in *championi*), in the more anterior placement of the umbones in *antarctica*, and the number of posterior teeth which is much greater in *antarctica*. It is not closely similar to any other South Atlantic species.

This species is named for Merrill E. Champion who for many years has given much time and energy to the study of Recent mollusks at the Museum of Comparative Zoology.

Records. In addition to the holotype from station 12, seven additional specimens were collected at station 14 (1703 fathoms, Cape Basin, about 14 miles northwest of Capetown, South Africa). They differ from the holotype in their smaller size and less iridescent periostracum but are identical in all other respects.

Tindaria antarctica Thiele and Jaeckel, 1931

One living specimen of this species was collected at R/V VEMA biology station 47 (2054 fathoms, western end of the Atlantic Indian Antarctic Basin, about 60 miles south of South Georgia) and another living specimen and two extra valves were collected at station 48 (1902 fathoms, about 100 miles southeast of South Georgia). They agree perfectly with the description and figure in Thiele and Jaeckel (1931, pl. 8, fig. 71) except for a slight difference in the number of teeth (8 anterior and 18 posterior instead of 6 and 20 as in *antarctica*) and their somewhat smaller size (8.5 mm. long instead of 11.5 mm.). The type locality of *antarctica* is VALDIVIA station 152 (2535 fathoms at 63°16.5′ S., 57°51′ E., eastern end of the Atlantic Indian Antarctic Basin).

Clencharia, new subgenus

Type species: *Tindaria* (*Clencharia*) *diaphana* Clarke.

Shells small, ovate, thin, transparent and with numerous flattened taxodont teeth. Pallial sinus well developed. Taxodont teeth wedge shaped and flattened laterally. Sculpture concentric and microscopic.

Clencharia differs from *Tindaria* (*sensu stricto*) principally in the form of the teeth, the sculpturing and the thickness and transpareney of the shell. The teeth in *Clencharia* are flattened and rectangular in cross-section while those of *Tindaria* are V-shaped in cross-section. The sculpturing in *Clencharia* is microscopic; in *Tindaria* it is not microscopic and is often prominent. The shell of *Clencharia* is very thin, diaphanous and transparent while that of *Tindaria* is relatively thick and not transparent.

This subgenus is named in honor of Dr. William J. Clench, a fine teacher and an outstanding authority on mollusks with whom the author has had the privilege of being associated.

Tindaria (Clencharia) diaphana, new species
Plate 1, figure 2

Shell small (5.6 mm. long), sub-ovate, inflated, nearly smooth, very thin, transparent and with a weak hinge plate bearing about 15 flattened chisel-shaped teeth. Valves completely transparent and clearly exhibiting the entire animal within. Outline sub-ovate, broadly rounded postero-ventrally and ventrally, gradually rounded and straighter dorsally and more sharply curved anteriorly and postero-dorsally. Umbones rounded, inflated, and projecting above the hinge line at a point about 30 per cent of the distance from anterior to posterior. Sculpture consisting only of microscopic concentric lines and ridges of growth. Periostracum very thin, transparent and iridescent. Ligament very thin, extending posteriorly from under the umbones. Larval valves tiny and white. Interior smooth except for microscopic growth lines, glossy, and exhibiting well marked muscle scars, pallial line and pallial sinus. Shell margin smooth. Hinge plate compressed and narrow except a little wider anteriorly and somewhat thickened and sigmoid under the beaks, but otherwise following the dorsal margin of the valves. Hinge plate bearing six anterior and nine posterior dorso-ventrally compressed, chisel-shaped taxodont teeth. Teeth well developed but rather small (largest near the center of each row) and becoming obsolete and not meeting under the beaks. Umbones excavated.

	length (mm.)	height (mm.)	width (mm.)
holotype, station 52	5.6	4.1	2.8
paratype, station 52	5.7	4.2	2.9
paratype, station 52	4.4	3.2	1.9

Types. The holotype and two paratypes were taken at R/V VEMA biology station 52 (2711 fathoms, Agulhas Basin, about 800 miles southwest of Capetown, South Africa). The holotype (with a flake of orange paint from the dredge inside the shell) is in the Museum of Comparative Zoology, no. 224965. The paratypes are in the National Museum of Canada, no. 4741.

Remarks. Tindaria (*Clencharia*) *diaphana* is characterized by its frail, transparent, bulbous shell and by its peculiar chisel-shaped teeth. It can be differentiated from all other fragile taxodonts (e.g. *Glomus*, *Phaseolus*, *Sarepta*, etc.) by the general shape of the shell and the form of the teeth. For differences between this and *Tindaria* (*sensu stricto*), see under *Clencharia*.

Records. Known only from station 52. See under 'Types'.

Family NUCULANIDAE

Genus NUCULANA Link 1807

Type species: *Arca rostrata* Chemnitz (= *Leda pernula* Müller), by monotypy.

NUCULANA ULTIMA Smith 1885

Nuculana ultima Smith 1885, Challenger Report, Lamellibranchs, p. 324, text fig. (2740 fms., southwest of Canary Islands).

Leda (*Ledella*) *modesta* Thiele and Jaeckel 1931, Muscheln der deutschen Tiefsee-Expedition, p. 202, pl. 2, fig. 30 (1245 fms., Gulf of Guinea).

Leda (*Ledella*) *spreta* Thiele and Jaeckel 1931, *loc. cit.*, p. 203, pl. 2, fig. 32 (69 fathoms, Agulhas Bank).

Living specimens of *Nuculana ultima* were taken by the VEMA at stations 12, 23, 47, 51, and 52 (2504 to 2805 fathoms; Argentine, Angola and Agulhas basins and Scotia Sea). Several specimens were collected at each locality and large series were obtained at stations 12 and 52. The species is quite variable as to the presence or absence of a short rostrum, in the strength of the hinge plate, and especially in the thickness and inflation of the shell. Apparently when the species reaches adult length and height further growth takes place at the inner edge of the shell and it becomes progressively more obese. At the same time the whole shell thickens. In one lot (station 52) this has resulted in sufficient variation so that width/height ratios vary from .65 to .95 among adult specimens. *Nuculana ultima* Smith was described from a single specimen, and *modesta* and *spreta* Thiele and Jaeckel were also represented by only a few shells. These authors apparently obtained isolated examples of an unusually variable species and under such conditions they appeared distinct.

Subgenus THESTYLEDA Iredale 1929

Type species: *Leda ramsayi* Smith, original designation.

NUCULANA (THESTYLEDA) LOUISEAE, new species

Plate 1, figure 7

Shell medium sized (19 mm.), rather thin, narrow, rostrate, compressed, strongly sculptured and with numerous oblique, lamellar, taxodont teeth. Valves ovate anteriorly, with a long, arcuate, posterior rostrum and with small umbones placed close together and about 30 per cent of the length from the anterior

end. Rostrum narrow, truncate and bilobed distally, concave dorsally and ventrally and surmounted with two prominent, curved carinae on each valve running from the umbones to the distal end. The lower carina is larger and becomes double as it proceeds posteriorly. Carinae crossed by crisp, narrow, wave-like ridges, which on the upper carina are convex and on the lower carina are concave dorsally and sharply convex ventrally. Ridges continuing on the disc as narrow, rounded, closely spaced ribs following lines of growth. Between the long, thin, external ligament and the rostral carinae is a smooth, almost unsculptured area, extending from the umbo and becoming narrow and obsolete near the posterior end. Periostracum thin, light grayish yellow. Inner surface of valves mostly white, nacreous, showing the external sculpturing and numerous, weak radial lines. Anterior muscle scar circular and faint, posterior scar irregularly ovate, and pallial line indistinct. Hinge teeth compressed, v-shaped, lamellar, very oblique, rather high and firmly interlocking, about 12 anteriorly and 20 posteriorly. Internal resilium in two separate but adjacent parts, the anterior part small and round, the posterior part large and saddle shaped. Umbones not excavated.

	length (mm.)	height (mm.)	width (mm.)
holotype, station 12	19.0	7.0	3.5

Types. The holotype, an unique specimen, was collected at R/V VEMA biology station 12 (2805 fathoms, Argentine Basin, about 1000 miles east-southeast of Buenos Aires, Argentina). It is in the Museum of Comparative Zoology, no. 224958.

Remarks. Nuculana louiseae is characterized by its very long and narrow rostrum and its peculiar sculpture. Apparently it is not closely related to any other living species. It is somewhat similar to *Leda longicaudata* Thiele 1912 from the western end of the Eastern Indian Antarctic Basin, but in that species the rostrum is less extended, differently sculptured, and convex ventrally, while in *louiseae* it is concave. Compared with *Nuculana scalata* Prashad, from 500 fathoms near the Lesser Sunda Islands, northeast Indian Ocean, *louiseae* is higher and much more expanded anteriorly and with the umbones placed more posteriorly.

This species is named in honor of my wife, Louise R. Clarke, who has been a constant source of help in my work on the Mollusca.

Records. Known only from the type locality. See under 'Types'.

Genus SPINULA Dall 1908

Type species: *Leda* (*Spinula*) *calcar* Dall, original designation.

SPINULA SUBEXCISA (Dautzenberg and Fischer) 1897

Specimens which are here referred to *Spinula subexcisa* were collected at R/V VEMA biology stations 12, 14, 18, 19, 51 and 52 (1510-2805 fathoms, Argentine, Agulhas and Cape basins and Walvis Ridge).

Jeffreys (1876, 1879) recorded *Malletia excisa* (Philippi) in his reports on the VALOROUS and the LIGHTNING and PORCUPINE expeditions from 1125 to 1785 fathoms in the West Europe and Canaries basins. Comparisons with the Jeffreys Collection now in the United States National Museum show that the VEMA specimens cited here are identical to *M. excisa*, as Jeffreys understood it. Philippi's figure (1844, pl. 15, fig. 4) is of a different species however; it is a Tertiary fossil which is much more deeply excavated below the rostrum than is the VEMA species. This lack of agreement between the fossil and the recent abyssal species was recognized by Dautzenberg and Fischer (1897: 203) who proposed "var. *subexcisa*" for the modern species previously recorded by Jeffreys and others as *excisa*.

I consider that the present species is so different from the fossil *excisa* that it certainly deserves specific rank.

SPINULA MESSANENSIS ("Seguenza" Jeffreys) 1879

A single specimen was collected alive at R/V VEMA biology station 20 (2707 fathoms, Angola Basin, about 675 miles west of Walvis Bay, South-West Africa). It is very close to *messanensis* which has been recorded from the West Europe and Canaries Basin in 276 to 1731 fathoms (Locard 1897) and although it may later prove to be significantly (and subspecifically) different when more material is obtained this question cannot be decided now.

Order ANISOMYARIA

Family MYTILIDAE

Genus DACRYDIUM Torell 1859

Type species: *Modiola vitrea* Möller, by monotypy.

Dacrydium albidum Pelseneer 1903

Living specimens of what appear to be this species were collected at R/V VEMA stations 16, 18 and 25 (Cape, Angola and Guinea basins, 1660 to 2315 fathoms). They are almost completely transparent and reveal the entire animal within. In this they differ from *albidum*, and in a group so lacking in taxonomic characters this may be significant, but for the present they are considered as abyssal and depauperate representatives of that species.

Family PECTINIDAE

Genus Pseudamusium Mörch 1853

Type species: *Ostrea hybrida* Gmelin, subsequent designation, Dall 1898.

Pseudamusium pteriola (Melville and Standen) 1907

A single valve of this species was collected at R/V VEMA biology station 46 (2030 fathoms, Scotia Sea, about 60 miles south of South Georgia). The type locality of *pteriola* is: Scotia Bay, South Orkney Islands, 9 to 10½ fathoms. Apparently this valve is advectitious.

Genus Propeamussium de Gregorio 1883

Type species: *Pecten* (*Propeamussium*) *cecilae* de Gregorio, by monotypy.

Propeamussium (Parvamussium) octodecimliratum (Melville and Standen) 1907

One living specimen plus a fragment of what appears to be this species were taken at R/V VEMA biology station 51 (2507 fathoms, Agulhas Basin, about 1000 miles southwest of Capetown, South Africa). It differs from *octodecimliratum* in the possession of 13 instead of 18 internal ribs, but since it is only 4.3 mm. high (the holotype of *octodecimliratum* is 9.0 mm. high) this difference is probably attributable to age. Occasional specimens of *Propeamussium* (e.g. *P. dalli* Smith) interpolate additional ribs with growth, and this may occur in the present species. The type locality of *P. octodecimliratum* is: 2500 fathoms, 67°33′ S., 36°35′W., western end of Atlantic Indian Antarctic Basin.

Family LIMIDAE

Genus LIMATULA S. Wood 1839

Type species: *Pecten subauriculata* Montagu, subsequent designation, Gray 1847.

LIMATULA SIMILLIMA (Thiele) 1912

One valve of this species occurred at R/V VEMA biology station 14 (1703 fathoms, Cape Basin, about 400 miles northwest of Capetown, South Africa). It was perforated with a neat, round hole, apparently caused by a gastropod. Such perforations are rare among abyssal mollusks and this specimen is probably advectitious in the deep sea. The type locality is Gauss Station in the southwestern part of the Eastern Indian Antarctic Basin.

Order EULAMELLIBRANCHIA

Family THYASIRIDAE

Genus THYASIRA "Leach" Lamarck 1818

Type species: *Tellina flexuosa* Montagu, by monotypy.

THYASIRA FERRUGINOSA (Forbes) 1844

Living specimens were collected at VEMA stations 16, 22 and 47 (1660, 1675 and 2056 fathoms in the Cape and Angola basins and the Scotia Sea). They were particularly common at station 16. They closely resemble specimens of the wide-ranging North Atlantic archibenthal and abyssal species *T. ferruginosa,* and are tentatively referred to that species.

Order SEPTIBRANCHIATA

Family POROMYACIDAE

Genus POROMYA Forbes 1844

Type species: *P. anatinoidea* Forbes (= *P. granulata* Nyst), by monotypy.

POROMYA SUBLEVIS Verrill 1884

A single living specimen of *Poromya* which is apparently identical with Dall's holotype of *P. microdonta* (= *P. sublevis* Verrill) was collected at R/V VEMA biology station 25 (2315 fathoms, Guinea Basin, approximately 675 miles south of

Accra, Gold Coast). The type locality is in the North American Basin, 125 miles off Chesapeake Bay, Virginia, in 1685 fathoms. Dall (1889b) has extended the range of this species to "Patagonia" and "West America" but without station data or other explanation. These records need confirmation.

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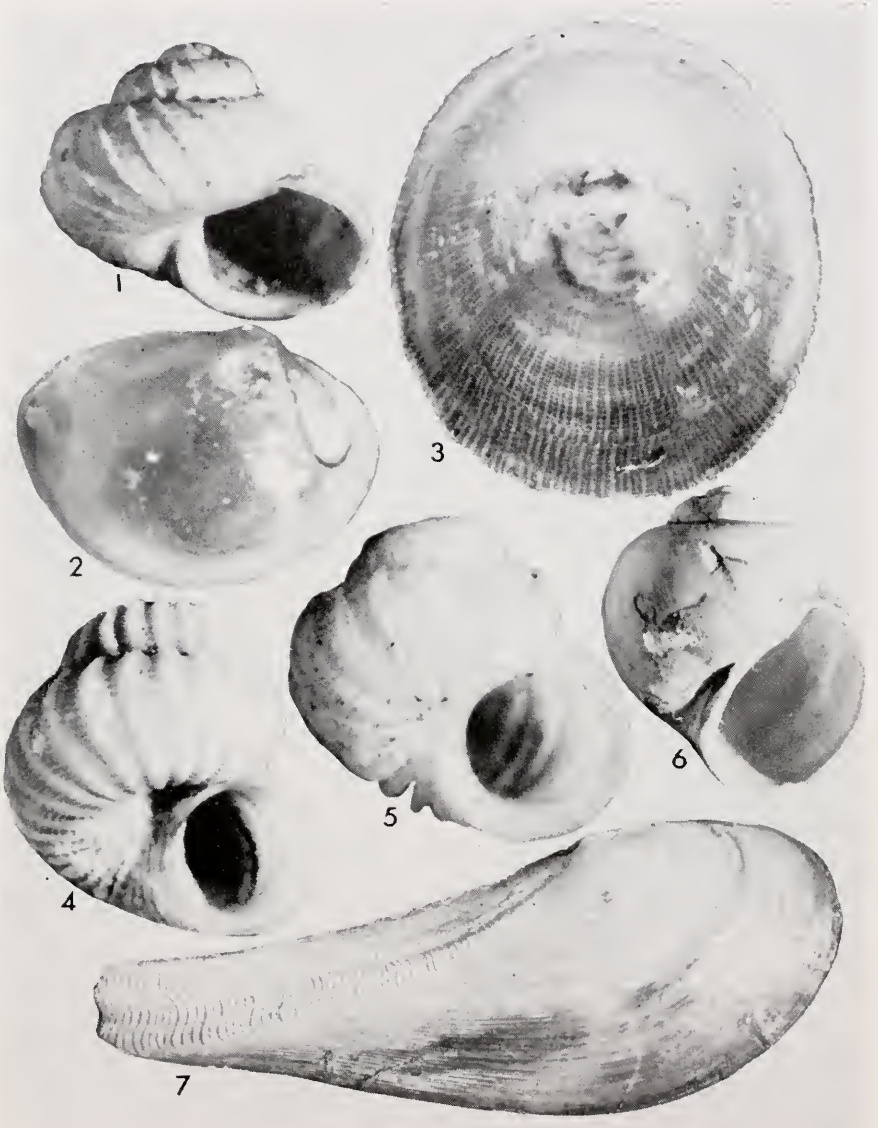

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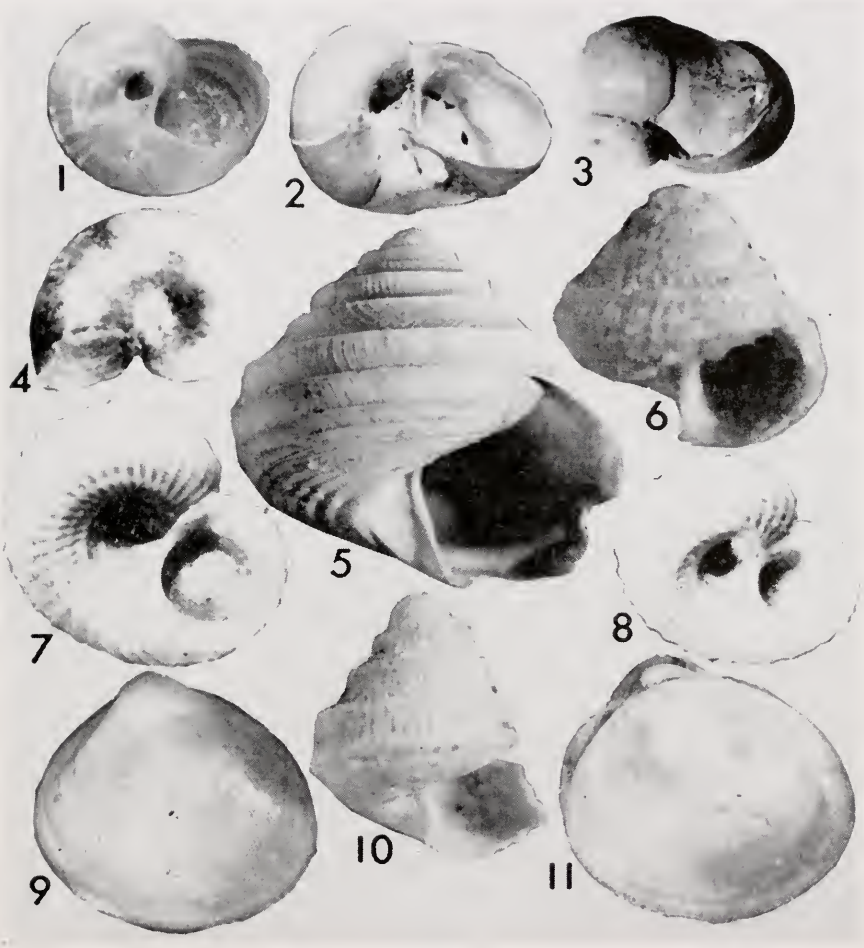

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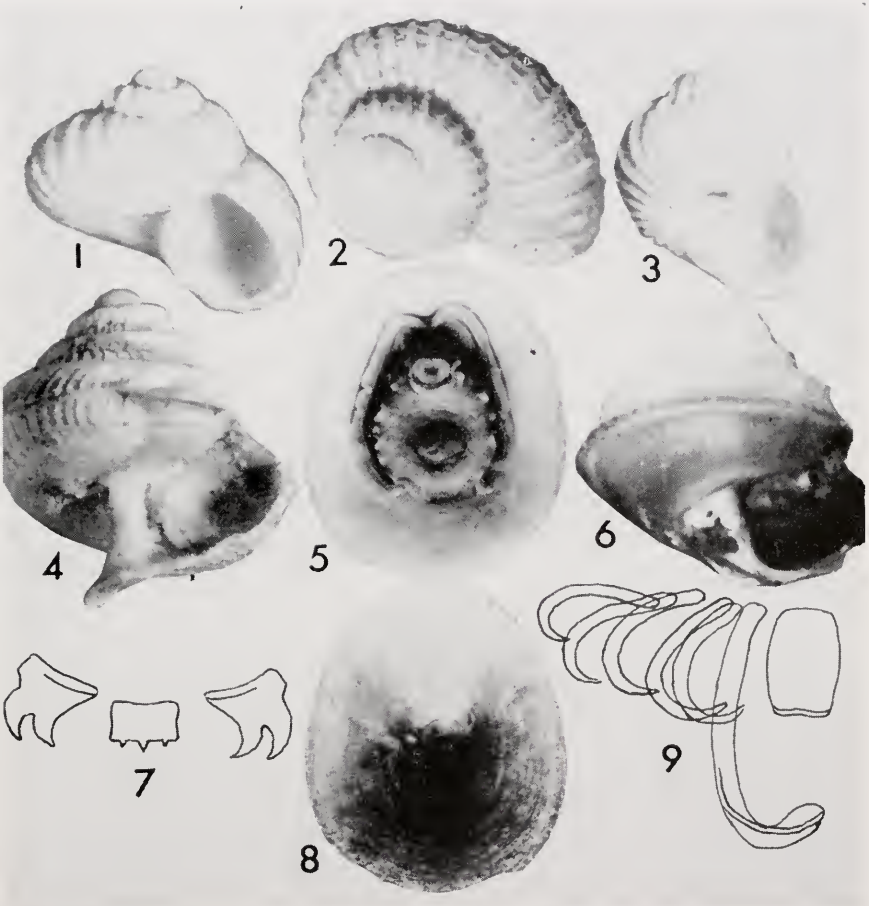

PLATE 4

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 125, No. 13

THE GENUS *MICRATHENA* (ARANEAE, ARGIOPIDAE) IN CENTRAL AMERICA

By Arthur M. Chickering
Albion College, Albion, Michigan

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
November, 1961

Publications Issued by or in Connection with the
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AT HARVARD COLLEGE

Bulletin (octavo) 1863 — The current volume is Vol. 125.

Breviora (octavo) 1952 — No. 145 is current.

Memoirs (quarto) 1864–1938 — Publication was terminated with Vol. 55.

Johnsonia (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 40 is current.

Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 2, no. 26 is current.

Proceedings of the New England Zoological Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

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The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution.

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Memoirs: Requests for some specific memoirs can be filled but no list is available.

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No. 13 — *The Genus Micrathena* (*Araneae, Argiopidae*) *in Central America*

By Arthur M. Chickering

The genus *Micrathena* Sundevall, 1833 with its numerous species, more or less conspicuous webbing, and often gaudy coloration constitutes an important segment of the arthropod fauna of Central America. For more than thirty years, during repeated visits to Panama and nearby regions, I have been collecting members of this genus with the intention of publishing the results of my study of all species appearing in my collections. Upon the advice of other araneologists I have recently extended my study to include the whole of Central America. In order to aid me in this work all specimens of the genus in the Museum of Comparative Zoology at Harvard College have been turned over to me for study. During the summer of 1958, while on a fellowship from the John Simon Guggenheim Memorial Foundation, I was able to work on the extensive collections in the British Museum (Natural History) where I had access to most of the material which furnished the basis for the work of the two Pickard-Cambridges published in the Biologia Centrali-Americana. A few days were also spent in the Oxford University Museum where a portion of the Pickard-Cambridge collection is kept.

Acknowledgements are due and gratefully rendered to the following named individuals and organizations for their numerous courtesies, support, and encouragement of my work for many years: The John Simon Guggenheim Memorial Foundation for its financial aid during two successive years; Dr. G. Owen Evans, Department of Zoology, British Museum (Natural History), and his staff of co-workers all of whom gave me very friendly encouragement and the loan of important specimens for the pursuit of my work; Professor G. C. Varley and his staff of co-workers at the Oxford University Museum who gave me access to valuable specimens for a brief period and then extended material on loan as a further aid; Dr. A. S. Romer, Director, Dr. P. J. Darlington, Jr., Curator of Insects, Dr. Herbert W. Levi, Associate Curator of Arachnology, and Miss Nelda E. Wright, Editor of Publications, all of the staff of the Museum of Comparative Zoology at Harvard College.

The problem of evolution and interspecific relationships in the genus *Micrathena* are exceedingly interesting, often complex, baffling, and difficult to trace. Females tend to exhibit a high

degree of abdominal spination involving many different patterns, and often show strongly contrasting and variable color patterns. The males, on the other hand, as adults usually lack definite spines, exhibit much less gaudy coloration, are greatly reduced in size, and possess a set of complex variations in the minute structure of their secondary sexual organs and related parts. The high degree of sexual dimorphism has made it extremely difficult to match adult males with the proper females. Moreover, adult males are relatively infrequent in collections. When young the sexes often resemble each other rather closely and this fact can sometimes be used as an aid in matching the sexes accurately.

F. Pickard-Cambridge (1904) included a total of thirty-one species in his treatment of the genus *Micrathena*. One of these (*A. fericulum* O. P.-Cambridge) has been transferred to the genus *Ildebaha* Keyserling. Of the remaining thirty species, five had both sexes fully recognized, seven were known only from males, and the remaining nineteen were known only from females.

So far as I have been able to determine up to the present time, a total of forty species of the genus *Micrathena* have been more or less definitely reported from Central America. Eight of these were males unassociated with females; six species included both sexes; twenty-six species were known only from females. As will be shown in the appropriate places in this paper, all four species described as new by Chamberlin and Ivie (1936) have been synonymized with already known species. It now seems quite certain that *M. sedes* (Getaz) is really *M. sexspinosa* (Hahn). It is now generally known that *M. cornigera* (O. P-Cambridge) is the male of *M. sexspinosa* (Hahn) and that *M. longicauda* (O. P.-Cambridge) is the male of *M. horrida* (Taczanowski). It has now been possible to complete the identification of the male of *M. schreibersi* (Perty). *M. clypeata* (Walek.), until recently considered to be distinctly a South American species, is now known to be well established in Panama. In addition to the changes noted above, I have been obliged to recognize and describe nine new species, thus bringing the revised list to forty-three as now reported from Central America. Among these are twenty different kinds of males, nine of which are still unassociated with the proper females. The complete list as the

species are understood at the present time may be given as follows:

M. bimucronata (O. P.-Cambridge), 1899
M. brevipes (O. P.-Cambridge), 1890
M. catenulata F. P.-Cambridge, 1904
M. clypeata (Walck.), 1805
M. crassa (Keyserling), 1863
M. disjuncta sp. nov.
M. donaldi sp. nov.
M. duodecimspinosa (O. P.-Cambridge), 1890
M. fidelis (Banks), 1909
M. flaveola (C. L. Koch), 1839
M. funebris (Banks), 1898
M. furcula (O. P.-Cambridge), 1890
M. gladiola (Walck.), 1841
M. gracilis (Walck.), 1805
M. granulata F. P.-Cambridge, 1904
M. horrida (Taczanowski), 1873
M. inaequalis F. P.-Cambridge, 1904
M. insolita sp. nov.
M. macfarlanei sp. nov.
M. macilenta sp. nov.
M. militaris (Fabricius), 1775
M. mitrata (Hentz), 1850
M. mirifica sp. nov.
M. modica sp. nov.
M. molesta sp. nov.
M. parallela (O. P.-Cambridge), 1890
M. patruelis (C. L. Koch), 1839
M. petersi (Taczanowski), 1872
M. quadriserrata F. P.-Cambridge, 1904
M. saccata (C. L. Koch), 1836
M. sagittata (Walck.), 1841
M. schreibersi (Perty), 1833
M. serrata F. P.-Cambridge, 1904
M. sexspinosa (Hahn), 1822
M. spinulata F. P.-Cambridge, 1904
M. striata F. P.-Cambridge, 1904
M. subflava sp. nov.
M. subspinosa F. P.-Cambridge, 1904
M. trapa (Getaz), 1891
M. triserrata F. P.-Cambridge, 1904
M. uncata F. P.-Cambridge, 1904
M. vitiosa (O. P.-Cambridge), 1890
M. zilchi Kraus, 1955

Holotypes of all new species described in this paper will be deposited in the Museum of Comparative Zoology at Harvard College. *M. donaldi* sp. nov. is named for my son who accompanied me on two very pleasant and productive collecting trips to Panama. *M. macfarlanei* sp. nov. is named for Mr. D. Macfarlane, Commonwealth Institute of Entomology, with whom I was very pleasantly associated during my period of work in the British Museum (Natural History) in the summer of 1958.

Genus Micrathena Sundevall, 1833

A comprehensive definition of the genus *Micrathena* Sundevall is very difficult to draw up because of the great differences which exist between males and females and even among the two sexes themselves. For the present I am simply adopting what I consider to be the general understanding among araneologists at the present time. I cannot do better than to accept the definition essentially as given by Reimoser (1917) in his treatment of the whole genus as he understood it at the time of the publication of his paper.

No attempt is made to include all citations which have appeared in the literature on this genus. Only those which are considered as particularly pertinent are given here. Those who desire more extensive bibliographies are referred to Roewer (1942) and Bonnet (1957).

Because of unusual difficulties, no satisfactory key to the females in this genus has been worked out. This is in part due to the fact that puzzling variations in spination and some other features occur quite frequently. The accompanying key to the males should be an aid in identification of the different members of this sex.

Key to the Species of Micrathena *in Central America*

Males

1. With a ventral hook on first coxa and a corresponding ridge and groove on second femur (*clypeata, disjuncta, duodecimspinosa, furcula, macilenta, mitrata, parallela, patruelis*) 2

1a. Without any ventral hook on first coxa and without a corresponding ridge and groove on second femur (*brevipes, donaldi, gracilis, granulata, horrida, mirifica, modica, sagittata, schreibersi, sexspinosa, uncata, vitiosa*) 9

2. Carapace with three pairs of clearly defined dorsolateral foveae .... *clypeata*, p. 400
2a. Carapace without three pairs of clearly defined dorsolateral foveae (*disjuncta, duodecimspinosa, furcula, macilenta, mitrata, parallela, patruelis*) 3
3. Abdomen at least twice as long as wide (*duodecimspinosa, furcula, macilenta, mitrata, parallela*) 4
3a. Abdomen less than twice as long as wide (*disjuncta, patruelis*) 7
4. With palpal tibia considerably wider than long (*macilenta, mitrata, parallela*) 5
4a. With palpal tibia not notably wider than long (*duodecimspinosa, furcula*) 8
5. Abdomen with clearly evident spinules at posterior end (*macilenta, parallela*) 6
5a. Abdomen with no clearly defined spinules at posterior end .... *mitrata*, p. 435
6. Basal palpal tarsal hook nearly as broad at tip as long (Fig. 137) .... *parallela*, p. 443
6a. Basal palpal tarsal hook not nearly as broad at tip as long (Fig. 104) .... *macilenta*, p. 432
7. Abdomen nearly rectangular in outline (Fig. 143) .... *patruelis*, p. 445
7a. Abdomen more rounded laterally; not so nearly rectangular in outline (Fig. 26) .... *disjuncta*, p. 403
8. Abdomen with definite tubercles at posterior end, indicating suppressed spines .... *duodecimspinosa*, p. 408
8a. Abdomen without definite tubercles at posterior end, indicating suppressed spines .... *furcula*, p. 416
9. Abdomen slender, at least twice as long as broad (*brevipes, gracilis, granulata, horrida, modica, sagittata, schreibersi, sexspinosa, uncata*) 10
9a. Abdomen not so slender, about twice as long as broad or less than twice as long as broad (*donaldi, mirifica, vitiosa*) 18
10. Abdomen with a caudal-like extension (Figs. 75, 86; *gracilis, horrida*) 11
10a. Abdomen without any caudal-like extension (*brevipes, granulata, modica, sagittata, schreibersi, sexspinosa, uncata*) 12
11. Base of bulb of palpal tarsus with a rounded knob fitting into a corresponding concavity in the tarsal hook (Fig. 76) .. *gracilis*, p. 421
11a. Base of bulb of palpal tarsus without such a knob and corresponding concavity as in *gracilis* .... *horrida*, p. 424
12. Palpal tarsal hook extended into a long, distally curved, sickle-like structure (Fig. 180) .... *sexspinosa*, p. 456
12a. Palpal tarsal hook not extended into a distinctly sickle-like structure (*brevipes, granulata, modica, sagittata, schreibersi, uncata*) 13
13. Abdomen constricted in the middle and rounded posteriorly (Fig. 161) .... *schreibersi*, p. 452

13a. Abdomen not constricted in the middle nor smoothly rounded posteriorly (*brevipes, granulata, modica, sagittata, uncata*) 14
14. Palpal tibia extended distally into a pair of sharp spines (Fig. 156) ..... *sagittata*, p. 449
14a. Palpal tibia not extended distally into a pair of sharp spines (*brevipes, granulata, modica, uncata*) 15
15. Palpal tibia extended into a series of three bluntly rounded outgrowths (Fig. 7) ..... *brevipes*, p. 398
15a. Palpal tibia not extended into a series of three bluntly rounded outgrowths (*granulata, modica, uncata*) 16
16. Palpal tarsal hook a strongly chitinized and granulated plate (Figs. 81, 82) ..... *granulata*, p. 423
16a. Palpal tarsal hook without a strongly chitinized and granulated plate; tarsal hook tending toward the type more frequently found in the genus (*modica, uncata*) 17
17. First femur with a group of modified ventral spines near middle of the segment (Fig. 203) ..... *uncata*, p. 466
17a. First femur without the group of modified spines near middle of segment ..... *modica*, p. 439
18. Abdomen with four pairs of definite but small spines (Fig. 31) ..... *donaldi*, p. 405
18a. Abdomen without any definite spines (*mirifica, vitiosa*) 19
19. Palpal tarsal hook extended into a quadrate, concave, finely granulose plate; with remains of three pairs of spines in the form of tubercles on abdomen ..... *vitiosa*, p. 466
19a. Palpal tarsal hook not extended into a quadrate, concave, finely granulose plate; abdomen without visible remains of tubercles on abdomen ..... *mirifica*, p. 437

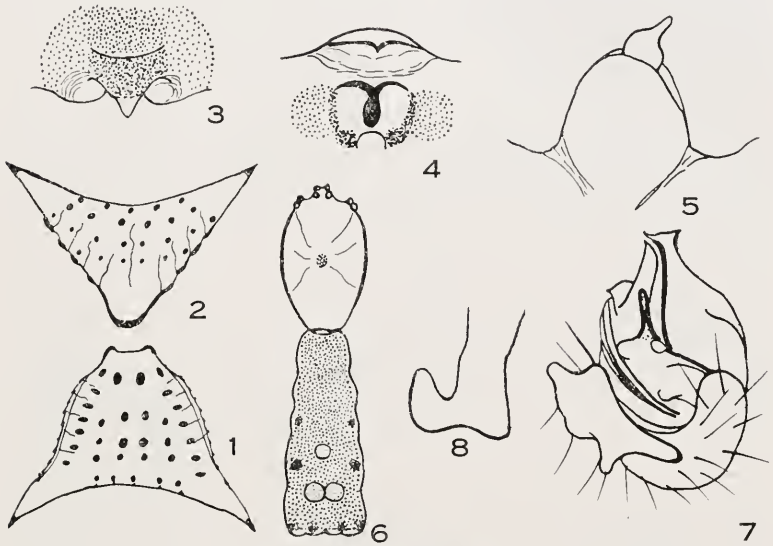
Micrathena bimucronata (O. P.-Cambridge), 1899

(Figures 1-5)

Acrosoma bimucronatum O. P. Cambridge, 1899
M. bimucronata F. P.-Cambridge, 1904
M. bimucronata Petrunkevitch, 1911
M. bimucronata Reimoser, 1917
M. bimucronata Chickering, 1931
M. bimucronata Mello-Leitao, 1932
M. bimucronata Roewer, 1942
M. bimucronata Bonnet, 1957

Several specimens of this species in the British Museum (Natural History) from Guatemala have been examined and found to agree well with specimens from Costa Rica and Honduras now in the collections of the Museum of Comparative Zoology at Harvard College. The male is still unknown. One of the specimens

in the collection of the Museum of Comparative Zoology has been selected as the hypotype from which the following facts have been derived: Total length 5.85 mm.; the abdomen has a short conical tubercle at each anterolateral corner (one specimen was found to have these tubercles drawn out into short spines thus illustrating the variability of the species) and a long stout spine at each posterolateral angle (Figs. 1, 2); the carapace has a



External Anatomy of *Micrathena*

Figures 1-5, *M. bimucronata*

Figures 6-8, *M. brevipes*

Fig. 1. Abdomen of female, dorsal view.

Fig. 2. Posterior surface of abdomen to show appearance of spines.

Figs. 3-5. Epigynum; from below, posterior surface, and right lateral view, respectively.

Fig. 6. Body of *M. brevipes*, dorsal view.

Fig. 7. Right palpal tarsus and tibia.

Fig. 8. Palpal tarsal hook, more enlarged.

well defined central fovea and two pairs of moderately clear dorsolateral foveae; the characteristics of the epigynum are shown in Figures 3-5. The species is now known from Guatemala, Costa Rica and Honduras.

Micrathena brevipes (O. P.-Cambridge), 1890

(Figures 6-8)

Acrosoma brevipes O. P.-Cambridge, 1890
A. brevipes Keyserling, 1892
M. brevipes F. P.-Cambridge, 1904
M. brevipes Petrunkevitch, 1911
M. brevipes Reimoser, 1917
M. brevipes Petrunkevitch, 1925
M. brevipes Chickering, 1931
M. brevipes Roewer, 1942
M. brevipes Bonnet, 1957

This species was reported from Honduras in 1931 (Chickering) but the specimens seen at that time are not now in the collection and cannot, therefore, be re-examined for accuracy of determination. My only opportunity to study the species carefully came during my period of work in the British Museum (Natural History) in the summer of 1958. Two specimens are now in the vial marked "type" but both abdomens are detached and one may not belong to *M. brevipes* (O.P.-Cambridge). Both cephalothoraces and attached parts are in good condition. The abdomen (Fig. 6) is injured but appears to be similar to that of the male of *M. sexspinosa*. The chief features of the palpal tarsus and tibia are shown in Figures 7 and 8. Keyserling's description (1892) appears to be accurate and detailed. Total length about 4.5 mm. The legs appear to be devoid of significant spines. The first coxae lack the ventral hook and the second femora lack the corresponding ridges and grooves. The female remains unknown. The species appears to be widely distributed in Central America and has been reported from Mexico, Guatemala, Honduras, and Panama.

Micrathena catenulata F. P.-Cambridge, 1904

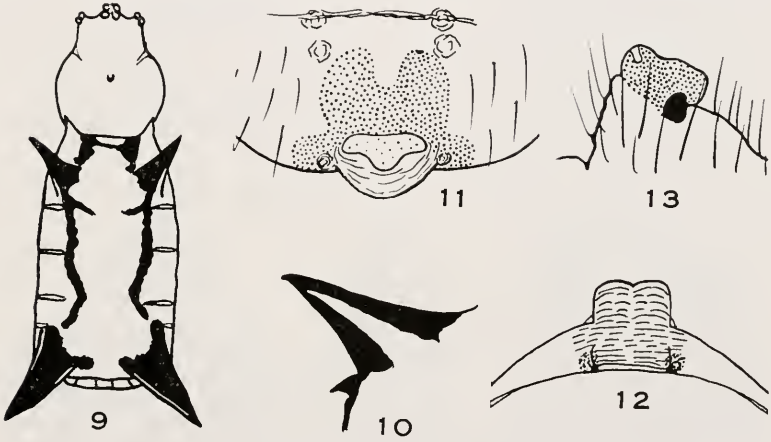
(Figures 9-13)

M. catenulata Petrunkevitch, 1911
M. catenulata Reimoser, 1917
M. catenulata Roewer, 1942
M. catenulata Bonnet, 1957

In the Nathan Banks collection in the Museum of Comparative Zoology I have found several females from Mexico which agree well with specimens in the Pickard-Cambridge collection in the

British Museum (Natural History). I also have two specimens collected by myself in Honduras. Two males were found with the females from Mexico but they are still considered to represent a separate species for reasons which will be given in some detail later in this paper.

Female hypotype. Total length 6.695 mm. One difference between the hypotype and the holotype is in respect to abdominal spines. F. P.-Cambridge stated that the "anterior marginal angles" of the abdomen were prominent but did not bear spines. Apparently this is a variable feature because spines occur in these regions in some specimens but not in all. Short anterior marginal spines are extended from the corners of the abdomen in the hypotype. There are also two pairs of relatively large robust spines in dorsal anterior and posterior positions as indicated in Figure 9. It was also stated in the original descriptions



External Anatomy of *Micrathena*

Figures 9-13, *M. catenulata*

Fig. 9. Dorsal view of body.

Fig. 10. Posterior spine and cusp; lateral view from right side.

Figs. 11-13. Epigynum from below, in posterior view, and in profile from right side, respectively.

that immature specimens have a short cusp below each posterior dorsal spine. I have found that this also sometimes occurs in mature females (Fig. 10). The head portion of the carapace is only moderately raised. The sternum is not notably produced

posteriorly. The features of the epigynum are shown in Figures 11-13. Color in alcohol: the Mexican and Honduran specimens are much lighter in color than the Guatemalan specimens available to F. P.-Cambridge. Apparently the black spots have been reduced and the white parts greatly extended as indicated in Figure 9.

Collection records. The specimens studied by F. P.-Cambridge were from Guatemala. Other specimens available to me in this study are from Escuintla, Chiapas, Mexico, with no date of collection given, and Lancetilla, Honduras, July, 1929.

Micrathena clypeata (Walckenaer), 1805

(Figures 14-20)

Epeira clypeata Walckenaer, 1805
M. clypeata Sundevall, 1833
M. clypeata, C. L. Koch, 1838
Plectana clypeata Walckenaer, 1841
M. clypeata Taczanowski, 1879
M. clypeata Simon, 1895
M. clypeata Petrunkevitch, 1911
M. clypeata Reimoser, 1917
M. planata Chamberlin and Ivie, 1936. New synonymy
M. clypeata Chickering, 1936
M. clypeata Roewer, 1942
M. planata Roewer, 1942. New synonymy.
M. clypeata Bonnet, 1957
M. planata Bonnet, 1957. New synonymy.

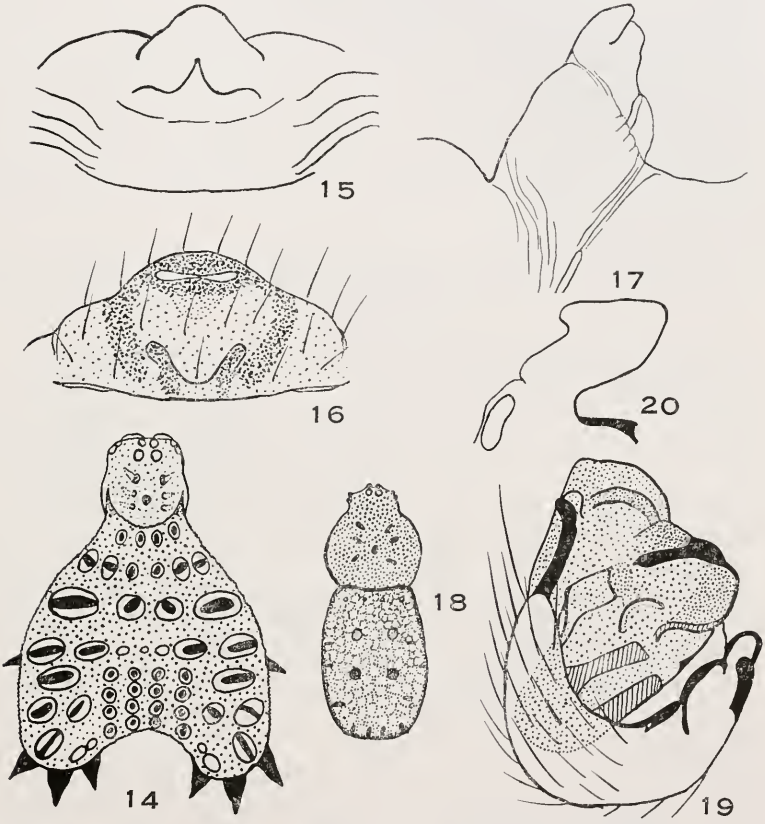
Until comparatively recently this species has been considered strictly South American, but is now known to be well established in Panama. Chamberlin and Ivie (1936) have given a detailed description of the species under the name *M. planata*.

Female hypotype. The extremely flattened form of the abdomen, the numerous smoothly chitinized dorsal abdominal spots, together with the ten abdominal spines (Fig. 14) should make identification certain. Figures 15-17 show the chief features of the epigynum.

Male hypotype. Total length 3.9 mm. With body extremely flattened (Fig. 18); with a complete but thin dorsal abdominal shield. The first coxa has a distal, ventral, retrolateral hook and the second femur has a corresponding groove and ridge near its proximal end nearly dorsal in position but on the prolateral surface. Palp: the tarsal hook has a characteristic form; this

and other features of the organ are shown in Figures 19 and 20.

Collection records. All of my records of this species in Panama have come from Barro Colorado Island, C. Z. The female hypotype was taken in August, 1954; the male hypotype in August, 1950. Two other males are in the collection: July,



External Anatomy of *Micrathena*

Figures 14-20, *M. clypeata*

Fig. 14. Dorsal view of body of female.

Figs. 15-17. Epigynum from below, in posterior view, and in profile (more enlarged), respectively.

Fig. 18. Dorsal view of body of male.

Fig. 19. Palpal tarsus of male.

Fig. 20. Palpal tarsal hook, retrolateral view (more enlarged).

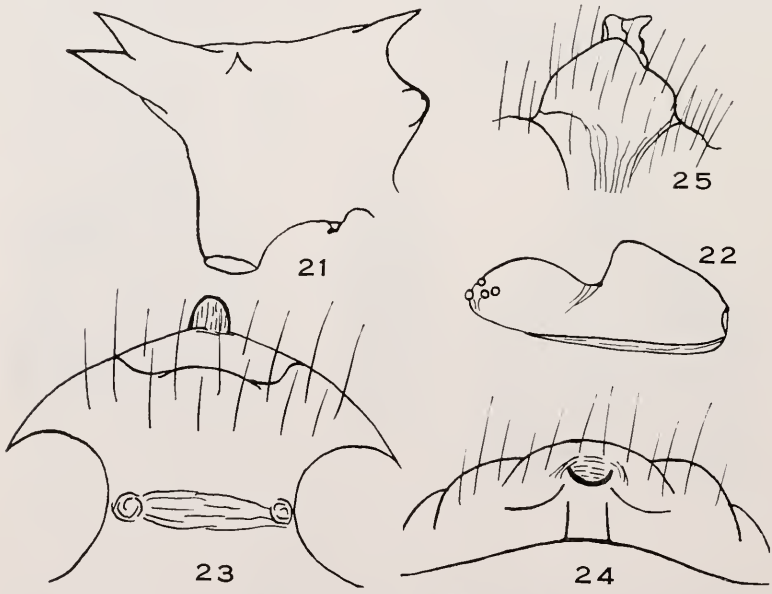
1924 (Banks) and July, 1936. Females have been taken from June to August, 1934, 1936, 1950, and 1954. Chamberlin and Ivie (1936) reported both sexes from my collection of 1928.

Micrathena crassa (Keyserling), 1863

(Figures 21-25)

Acrosoma crassum Keyserling, 1863
A. crassum Keyserling, 1892
M. crassa Simon, 1895
M. crassa Petrunkevitch, 1911
M. crassa Reimoser, 1917
M. crassa Petrunkevitch, 1925
M. crassa Roewer, 1942
M. crassa Bonnet, 1957
M. crassa Chickering, 1960

Petrunkevitch (1925) reported this species from Panama but it has not appeared in my collections nor have I found it recorded



External Anatomy of *Micrathena*

Figures 21-25, *M. crassa*

Fig. 21. Abdomen, lateral view.

Fig. 22. Cephalothorax, lateral view.

Figs. 23-25. Epigynum; from below, posterior view, and in profile, respectively.

by any other worker. During the summer of 1958 I had an opportunity to study the species in the Keyserling collection in the British Museum (Natural History) and I have commented on it elsewhere (1960). The most significant features of the species may be given as follows: There is considerable variation in the size of the females with the length varying from about 7.6 to 8.5 mm.; head and thorax well separated by a deep transverse groove; the median thoracic fovea is clearly defined; behind the median fovea the thorax rises very sharply into a pronounced gibbosity (Fig. 22); there are no clearly defined dorsolateral foveae; sternum only moderately convex; abdomen with four pairs of spines as shown in Figure 21; features of the epigynum as shown in Figures 23-25. Collection records are restricted to Colombia and Panama. The male is still unknown.

Micrathena disjuncta sp. nov.

(Figures 26-30)

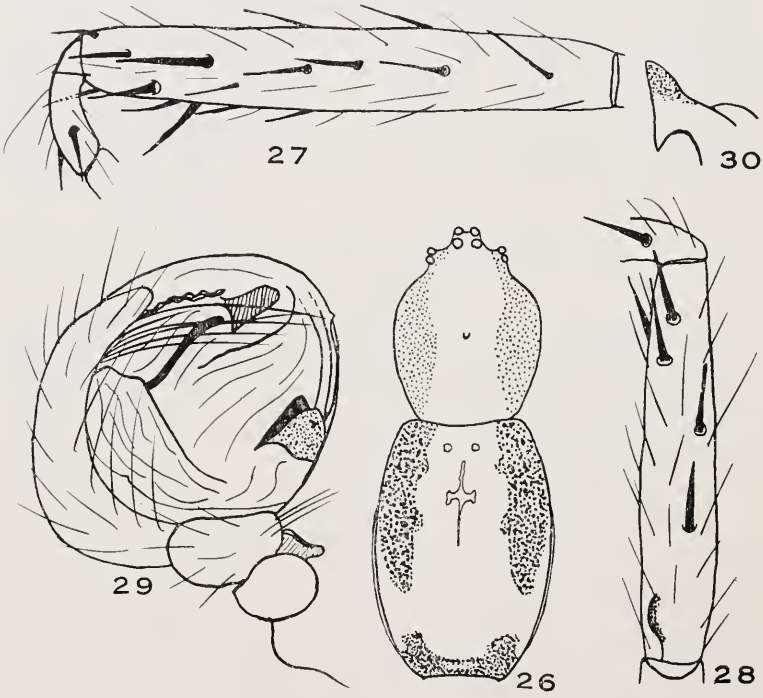
Male holotype. Total length 3.705 mm. Carapace 1.755 mm. long, 1.24 mm. wide opposite interval between second and third coxae where it is widest; .66 mm. tall shortly behind well defined central fovea; rises gently from just behind PME to this region and then descends to posterior border.

Eyes. Eight in two rows as usual. Seen from above, posterior row moderately recurved, anterior row strongly recurved. Seen from in front, anterior row very slightly recurved, posterior row gently procurved, all measured by centers. Ocular tubercles moderately well developed. Central ocular quadrangle only slightly wider behind than in front, slightly wider behind than long. Ratio of eyes AME : ALE : PME : PLE = 5 : 5 : 6.5 : 5 (long diameters used when there are differences). AME separated from one another by nearly two diameters, from ALE by about three diameters. PME separated from one another by nearly five-fourths of their diameter, from PLE by nearly three times their diameter. Laterals only separated by a broad line. Height of clypeus equal to a little more than twice the diameter of AME.

Chelicerae, Maxillae, and *Lip.* All apparently normal to males of the genus. Fragility of the specimen prevents close examination of such structures as teeth along the fang groove but details appear to be unnoteworthy for the proper description of the holotype.

Sternum. Simple scutiform; moderately convex; terminates bluntly between fourth coxae which are separated by about one-half of their width.

Legs. 1423. Width of first patella at "knee" .16245 mm., tibial index of first leg 10. Width of fourth patella at "knee" .11913 mm., tibial index of fourth leg 10.



External Anatomy of *Micrathena*

Figures 26-30, *M. disjuncta*

Fig. 26. Dorsal view of body of male.
Fig. 27. Right first femur, prolateral view.
Fig. 28. Right second femur, prolateral view.
Fig. 29. Male palpal tarsus.
Fig. 30. Palpal tarsal hook, more enlarged.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	1.540	.506	.990	.924	.462	4.422
2.	1.320	.440	.726	.748	.400	3.634
3.	.836	.264	.440	.418	.330	2.288
4.	1.540	.396	.814	.770	.435	3.955
Palp	.198	.0975	.1300	——	.440	.866

With numerous robust spines on legs 1, 2, and 4; those on femora appear to be most significant (Figs. 27-28). First coxa with a ventral hook and second femur with the corresponding proximal, prolateral ridge and groove.

Palp. Most essential features shown in Figures 29 and 30. Both tibia and patella are very short and without special modifications. Tarsal hook similar to that found in several other species.

Abdomen General shape shown in Figure 26. Poorly developed tubercles at posterior end may represent suppressed spines which show in immature males and in adult females.

Color in alcohol. Carapace yellowish white in a broad central stripe with a broad dusky stripe on each side (Fig. 26). Legs yellowish with variations. Mouth parts and sternum nearly white. Abdomen: dorsum with a broad, central, broken, white stripe and a semi-transparent cross in the middle; nearly black across posterior end and on each side a nearly black stripe (Fig. 26); just lateral to the black stripe are narrow, irregular, brownish stripes.

Type locality. The holotype male is from Barro Colorado Island, C. Z., January, 1958. No paratypes have appeared in my collection. The female is unknown.

Micrathena donaldi sp. nov.

(Figures 31-34)

Male holotype. Total length 4.68 mm. Carapace 1.917 mm. long; 1.125 mm. wide opposite second coxae where it is widest; median eyes on a prominent tubercle and lateral eyes on two confluent tubercles; only slightly raised behind median thoracic fovea.

Eyes. Eight in two rows as usual; viewed from above, both rows strongly recurved; viewed from in front, both rows procurved. Central ocular quadrangle wider behind than in front in ratio of 25 : 17, wider behind than long in ratio of 25 : 22.

Ratio of eyes AME : ALE : PME : PLE = 8 : 7 : 10 : 8. AME separated from one another by five-eighths of their diameter, from ALE by seven-fourths of their diameter. PME separated from one another by nearly their diameter, from PLE by three-halves of their diameter. LE separated from one another by about the diameter of AME. Height of clypeus equal to nearly twice the diameter of AME. Clypeus sharply slanted backward because of strong development of median ocular tubercle.

Chelicerae. Moderately well developed; parallel. Teeth along fang groove not observed because of danger of injury to holotype.

Maxillae and *Lip.* As usual in males of the genus, without noteworthy features.

Sternum. Moderately convex; strongly and irregularly corrugated throughout; sternal suture procurved; with well developed lateral sternal tubercles and low tubercles opposite coxae 1-3 and with a blunt, low tubercle at posterior end which is not extended between fourth coxae which are only slightly separated.

Legs. 4123. Width of first patella at "knee" .12996 mm., tibial index of first leg 10. Width of fourth patella at "knee" .11913 mm., tibial index of fourth leg 7.

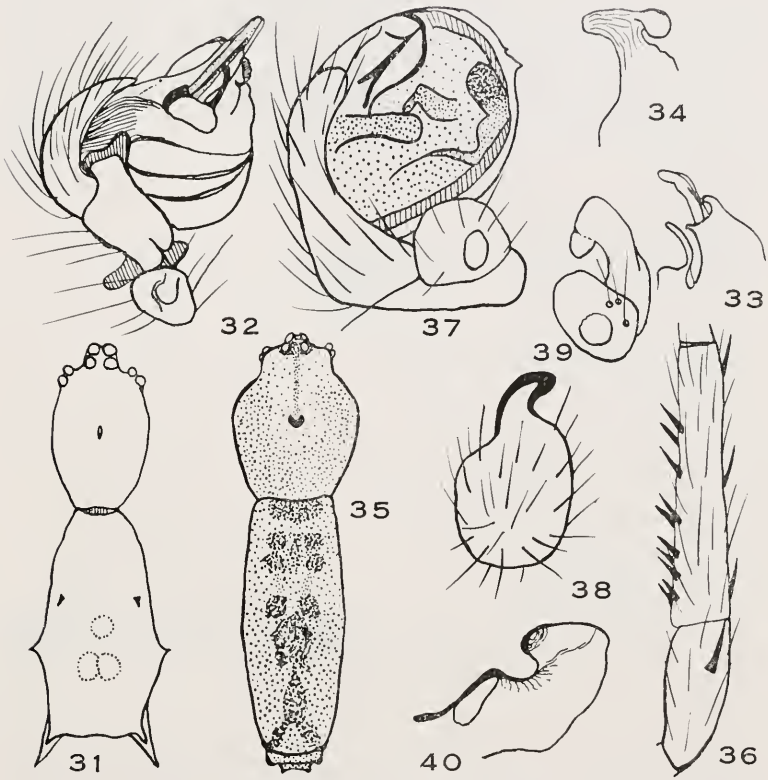
	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	1.170	.450	.845	.747	.520	3.732
2.	1.170	.410	.780	.650	.520	3.530
3.	.780	.270	.520	.440	.396	2.406
4.	1.625	.390	1.200	1.105	.625	4.945
Palp	.528	.176	.396	——	.726	1.826

Leg spines very sparsely and poorly developed. Coxal ventral hook and corresponding second femoral groove and ridge lacking.

Palp. General characters like those of male of *M. sagittata* but with tibia resembling that of *M. brevipes* (Figs. 32-34). The tibia appears to be quite distinctive and the same can be said for the tarsal hook.

Abdomen. General form shown in Figure 31. Abdominal spines much more prominent than usual in mature males; two posterior pairs are relatively large and conspicuous; there is a pair of short marginal spines somewhat behind the middle and another pair of very small dorsal spines somewhat in front of the middle; these suggest that the female should be found among

those with four pairs of more or less conspicuous abdominal spines such as *M. fidelis* (Banks).



External Anatomy of *Micrathena*

Figures 31-34, *M. donaldi*

Figures 35-40, *M. duodecimspinosa*

Fig. 31. Dorsal view of body of male.

Fig. 32. Left palpal patella, tibia, and tarsus, nearly prolateral view.

Fig. 33. Distal end of palpal conductor and associated structures; different view from that in Fig. 32.

Fig. 34. Palpal basal tarsal hook.

Fig. 35. Dorsal view of male allotype.

Fig. 36. Right second patella and tibia, prolateral view.

Fig. 37. Left palpal tibia and tarsus.

Fig. 38. Posterior surface of cymbium and tarsal hook from a paratype.

Fig. 39. Palpal tibia and tarsal hook.

Fig. 40. Another view of tarsal hook more enlarged; from a paratype.

Color in alcohol. Legs dark brown, almost black, above, but yellowish below. Carapace and sternum a dark mahogany brown. Abdomen: dorsum with three whitish spots as shown in Figure 31; with remaining surface a mosaic of black, whitish, brown, much streaked and dotted.

Type locality. Holotype male from Barro Colorado Island, C. Z., August, 1936. Two paratype males from the same locality, July, 1936. Mr. Banks collected one male in the same locality, July, 1924.

Micrathena duodecimspinosa (O. P.-Cambridge), 1890

(Figures 35-45)

Acrosoma 12-spinosum O. P.-Cambridge, 1890
Acrosoma 12-spinosa Keyserling, 1892
M. 12-spinosa F. P.-Cambridge, 1904
A. 12-spinosa Banks, 1909
M. duodecimspinosa Petrunkevitch, 1911
M. duodecimspinosa Reimoser, 1917
M. duodecimspinosa Chickering, 1936
M. duodecimspinosa Roewer, 1942
M. duodecimspinosa Kraus, 1955
M. duodecimspinosa Bonnet, 1957

Females of this species have been well described by Keyserling (1892), F. P.-Cambridge (1904), and Reimoser (1917). Abdominal spines are probably the best single clues to identification.

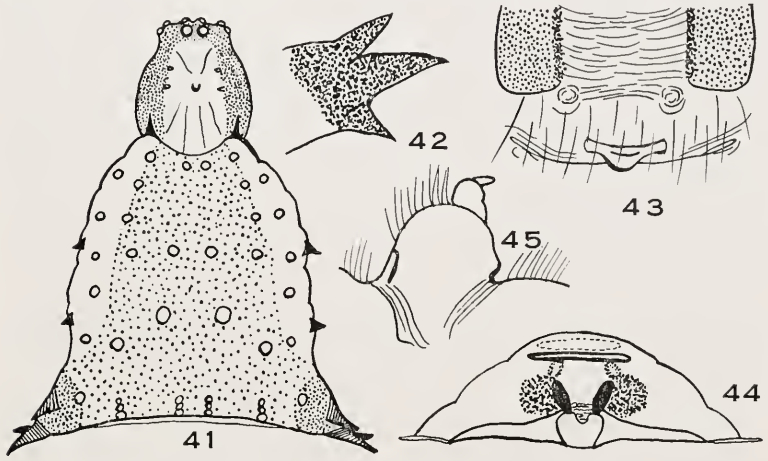
Female hypotype. Total length 7.475 mm. The salient features of body form are shown in Figures 41 and 42. In all of my Panamanian specimens the posterior spines are bright red. Features of the epigynum are shown in Figures 43-45.

Kraus (1955) has recently reported finding immature males but, so far as I have been able to determine, the mature male has never been described. For this reason, one of several males from Boquete, Chiriqui, Panama, has been selected as the allotype and described as follows:

Male allotype. Total length 4.973 mm. Carapace 1.885 mm. long, 1.43 mm. wide opposite interval between second and third coxae where it is widest; median fovea well developed; nearly level throughout from PME to posterior declivity (Fig. 35).

Eyes. Eight in two rows as usual; viewed from above, both rows strongly recurved; viewed from in front, anterior row slightly procurved and posterior row strongly procurved, all

measured by centers. Central ocular quadrangle wider behind than in front in ratio of 10 : 9; wider behind than long in about the same ratio. Ratio of eyes AME : ALE : PME : PLE = 6 : 4.5 : 8 : 5. AME separated from one another by about their diameter, from ALE by about 3.3 times their diameter. PME separated from one another by about their diameter, from PLE by 2.5 times their diameter. Laterals only slightly separated. Laterals on a rather marked tuberele. Height of clypeus equal to about 1.5 times the diameter of AME.



External Anatomy of *Micrathena*

Figures 41-45, *M. duodecimspinosa*

Fig. 41. Dorsal view of body of female.

Fig. 42. Spines at posterolateral corner of abdomen; viewed from posterior surface.

Figs. 43-45. Epigynum from below, posterior surface, and in profile (right side), respectively.

Chelicerae. Moderately well developed; essentially parallel; only slightly concave along outer border; basal boss small but clearly present; apparently four teeth on promargin and three on retromargin of well developed fang groove (observed on paratype to avoid injury to allotype).

Maxillae and *Lip.* As usual in the genus; details unnoteworthy.

Sternum. Only slightly convex; extended between all coxae and with posterior coxae only slightly separated.

Legs. 1423. Width of first patella at "knee" .18411 mm., tibial index of first leg 12. Width of fourth patella at "knee" .16245 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	1.430	.435	1.105	1.072	.585	4.627
2.	1.300	.422	.845	.910	.520	3.997
3.	.950	.325	.520	.550	.390	2.735
4.	1.820	.390	.910	.975	.500	4.595
Palp	.352	.132	.120	——	.572	1.176

There is a rather poorly developed ventral distal hook on the first coxa and a corresponding short prolateral proximal groove and ridge on the second femur. The first two pairs of legs are notably spiny, particularly the tibiae; the ventral spines on the second tibiae (Fig. 36) are short and robust. Trichobothria are prominent on the tibiae.

Palp. Both patella and tibia are very short. The features of the tarsus and tarsal hook are shown in Figures 37-40.

Abdomen. 3.120 mm. long; continued posterior to spinnerets about four-ninths of total length; remains of posterolateral spines, prominent in females, appear as short tubercles at posterior end. Other features as usual in the genus.

Color in alcohol. Legs brownish with variations; first two darkest. Chelicerae and palps yellowish with palpal tarsus light brown. Lip very dark brown like sternum. Maxillae dark grayish. Carapace brownish with variations. Abdomen with a dark irregular central series of spots and an irregular series of dorsolateral white spots making a pattern difficult to describe (Fig. 35); venter brownish dappled with yellowish white spots.

Collection records. The hypotype female is from Barro Colorado Island, C. Z., July, 1954. The allotype male is from Boquete, Chiriqui, Panama, July, 1939 at which time several paratype males were also taken. Females and immature males are in the collection from Barro Colorado Island, C. Z., June, 1934; June-July, 1936; June, 1939; July, 1954; January, 1958; France Field, C. Z., August, 1939. Several females are in the collection of the Museum of Comparative Zoology from Rio Jesus Maria, Costa Rica, January (Biolley and Tristan), and also from San Jose, Costa Rica (Valerio). The Cambridges had females from Mexico, Guatemala, and Panama.

Micrathena fidelis (Banks), 1909

(Figures 46-49)

Acrosoma fidelis Banks, 1909
M. fidelis Petrunkevitch, 1911
M. fidelis Reimoser, 1917
M. fidelis Roewer, 1942
M. fidelis Bonnet, 1957

This species is, apparently, known only from the holotype female which was very briefly described by its author without illustrations. These facts would seem to warrant a full description in accord with my usual formula. The description is taken directly from the original specimen.

Female holotype. Total length 7.02 mm. Carapace 2.34 mm. long; 2.015 mm. wide opposite second coxae where it is widest; with the median fovea as usual in the genus; cephalic portion somewhat convex behind PME, then transversely depressed just anterior to median fovea; conspicuously swollen just posterior to median fovea.

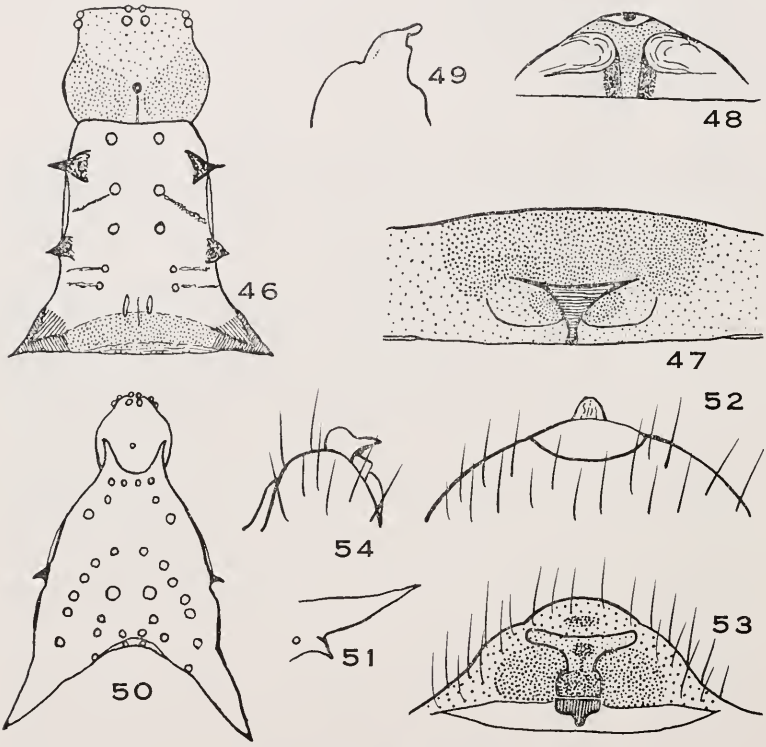
Eyes. Eight in two rows as usual; lateral eyes on a slightly raised tubercle; viewed from above, both rows moderately recurved; viewed from in front, anterior row slightly recurved, posterior row gently procurved; central ocular quadrangle wider behind than in front in ratio of 17 : 14, slightly wider behind than long. Ratio of eyes AME : ALE : PME : PLE = 4.5 : 5 : 7 : 3.5. AME separated from one another by their diameter, from ALE by four times their diameter. PME separated from one another by about five-sevenths of their diameter, from PLE by a little less than three times their diameter. Laterals almost in contact. Height of clypeus equal to a little less than the diameter of AME.

Chelicerae. Robust, vertical, nearly parallel, very convex in front, especially in proximal half; fang fairly robust and evenly curved; promargin of fang groove with four teeth, retromargin with three.

Maxillae and *Lip.* As usual in the genus; without noteworthy features.

Sternum. Elongate scutiform; quite convex throughout; not continued between coxae; with procurved sternal suture and moderately well developed sternal tubercles at each anterolateral corner. Posterior coxae separated by a little more than one-seventh of their width.

Legs. 1423. Width of first patella at "knee" .352 mm., tibial index of first leg 13. Width of fourth patella at "knee" .264 mm., tibial index of fourth leg 12.



External Anatomy of *Micrathena*

Figures 46-49, *M. fidelis*

Figures 50-54, *M. flaveola*

Fig. 46. Dorsal view of body of female.

Fig. 47-49. Epigynum from below, in posterior view, and in profile from right side, respectively.

Fig. 50. Dorsal view of body of female.

Fig. 51. Lateral view of spines at posterolateral corner of abdomen.

Figs. 52-54. Epigynum from below, in posterior view, and in profile from right side, respectively.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.210	.975	1.800	1.495	.775	7.255
2.	1.950	.855	1.365	1.280	.660	6.110
3.	1.300	.455	.785	.775	.600	3.915
4.	2.405	.715	1.430	1.495	.650	6.695

Legs with numerous spines and low tubercles from which hairs extend. Numerous trichobothria observed on tibiae and metatarsi.

Abdomen. General form and eight spines shown in Figure 46. Otherwise as usual in the genus.

Epigynum. In general quite similar to others in the genus but a profile view seems to show distinctive features (Figs. 47-49).

Type locality. The only specimen known to me is the holotype described by Banks (1909) and collected at Tablazo, Costa Rica (Tristan), September. The male remains unknown.

Micrathena flaveola (C. L. Koch), 1839

(Figures 50-54)

Acrosoma flaveolum C. L. Koch, 1839
Plectana flaveola Walckenaer, 1841
M. flaveola Petrunkevitch, 1911
M. flaveola Reimoser, 1917
M. flaveola Roewer, 1942
M. flaveola Bonnet, 1957

This species has caused me much concern and I still regard its status in Central America as somewhat questionable. The species has been reported from Mexico, Brazil, Dutch Guiana, and Venezuela. I am convinced that it has often been confused with *M. gladiola* (Walckenaer). Some of the specimens assigned to this species and to *M. gladiola* may well belong to other species, perhaps undescribed. I seem to have sound reasons for including the species among the Central American forms treated in this paper but I have had only one specimen for careful study and that was not in prime condition. The following facts are taken from this specimen:

Female hypotype. Total length to posterior border of abdomen between posterior spines 8.5 mm. (considerably larger than described by previous workers). The general form of the body

is shown in Figures 50 and 51. The carapace is somewhat gibbous just behind the central fovea; the sternum is finely rugulose and moderately convex but is not raised into a distinct cone as in *M. gladiola* (Walckenaer). The legs are badly fragmented and unmeasurable in this specimen. The spines appear as shown in Figures 50 and 51 and agree well with descriptions given by other authors who have had numerous specimens with which to work. The features of the epigynum are given in Figures 52-54. Males are still unknown. The hypotype female is from San Jose, Costa Rica, with no date of collection given.

Micrathena funebris (Banks), 1898

(Figures 55-59)

Acrosoma funebre Banks, 1898
M. funebris Petrunkevitch, 1911
M. funebris Reimoser, 1917
M. funebris Chamberlin, 1924
M. funebris Roewer, 1942
M. funebris Bonnet, 1957

Only the female of this species is known but there are now numerous specimens of this sex in the Museum of Comparative Zoology representing parts of the Banks and Chamberlin collections. Two of the specimens in the Banks collection are labelled "cotypes." In view of the brevity of the original description and the lack of accompanying figures, one of the "cotypes" has been selected and described in accord with my usual procedure.

Female hypotype. Total length 6.825 mm. Carapace 2.275 mm. long, 1.592 mm. wide opposite second coxae where it is widest; more slender than in many species (Fig. 55). Without additional noteworthy features.

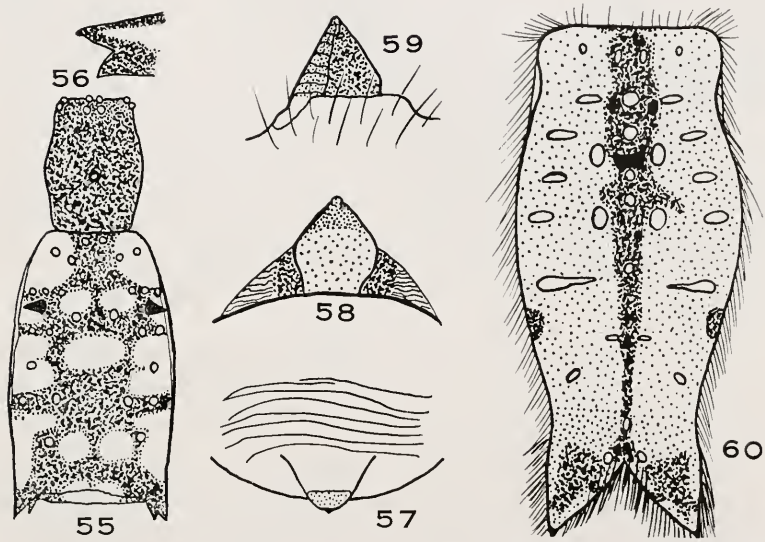
Eyes. Eight in two rows as usual; median eyes and laterals on low tubercles; viewed from above, both rows recurved; viewed from in front, anterior row gently recurved and posterior row procurved, both measured by centers; central ocular quadrangle wider behind than in front in ratio of 4 : 3, wider behind than long in ratio of 16 : 13. Ratio of eyes AME : ALE : PME : PLE = 7.5 : 5.5 : 10 : 6. AME separated from one another by eleven-sevenths of their diameter, from ALE by a little more than four diameters. PME separated from one another by about 1.5 times their diameter, from PLE by three diameters.

Laterals separated from one another by nearly the diameter of ALE. Height of clypeus nearly equal to twice the diameter of AME.

Chelicerae. Apparently as usual in the genus. Impossible to view the fang groove without serious injury to specimen.

Maxillae. Without noteworthy features.

Lip. Wider than long in ratio of 10 : 7; deeply grooved in basal fourth.



External Anatomy of *Micrathena*

Figures 55-59, *M. funebris*

Figure 60, *M. furcula*

Fig. 55. Body of female, dorsal view.

Fig. 56. Abdominal spines at posterolateral angle.

Figs. 57-59. Epigynum from below, from posterior view, and in profile from right side, respectively.

Fig. 60. Body of female in dorsal view.

Sternum. Elongate scutiform; longer than wide at anterior end in ratio of 23 : 18; sternal suture procurved; with low tubercles at anterolateral corners; with a prominent tubercle at posterior end; not extended between fourth coxae which are separated by about one-third of their width.

Legs. 4123. Width of first patella at "knee" .255 mm., tibial index of first leg 13. Width of fourth patella at "knee" .242 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	1.755	.650	1.250	1.300	.650	5.605
2.	1.625	.650	.975	1.235	.640	5.125
3.	1.170	.325	.715	.835	.520	3.565
4.	2.405	.585	1.430	1.235	.520	6.175

Apparently the leg spines were present in the usual manner but are now mostly lacking.

Abdomen. The general form of this part of the body is best shown in Figures 55 and 56. There are no anterior spines on the abdomen but six are present as shown. The color pattern appears to be characteristic and shows only minor variations among the numerous specimens from islands in the Gulf of California. Other features as usual in the genus.

Epigynum. Strongly tubercular; somewhat distinctive (Figs. 57-59).

Color in alcohol. In general, very dark brown or black with a rather distinctive pattern of white spots on the dorsum; essentially as described by the author of the species and with little change after long preservation.

Type locality. The original specimens came from Calmalli Mines, Sierra San Nicolas, and Mazatlan, Mexico (Tristan). The hypotype is from Mazatlan. There are many specimens from islands in the Gulf of California in the Chamberlin collection.

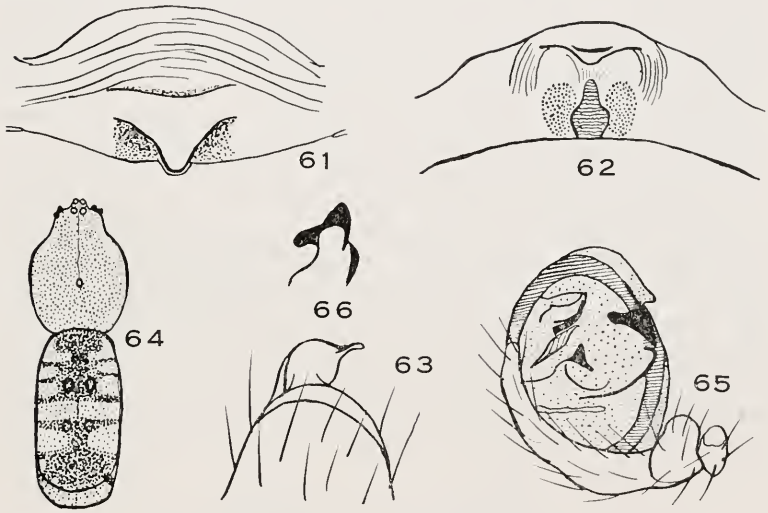
Micrathena furcula (O. P.-Cambridge), 1890

(Figures 60-66)

Acrosoma furcula O. P.-Cambridge, 1890
A. furcula Keyserling, 1892
M. furcula Simon, 1895
M. furcula F. P.-Cambridge, 1904
M. furcula Petrunkevitch, 1911
M. furcula Reimoser, 1917
M. furcula Banks, 1929
M. furcula Roewer, 1942
M. furcula Bonnet, 1957

Only the female has been known up to the present time. Now however, with the finding of immature males with a copious supply of hair as well as other revealing features the male can be positively identified. Banks was the first to report the female from Panama.

Female hypotype. Total length 11.375 mm. Carapace quite typical of the genus except that it is largely covered by a copious growth of long yellowish silky hair. The abdomen is also well supplied with hair but this is of a darker color and largely confined to the lateral margins and especially to the posterior furcula. The color as noted among the specimens available for study is quite variable but follows rather closely the



External Anatomy of *Micrathena*

Figures 61-66, *M. furcula*

Figs. 61-63. Epigynum from below, in posterior view, and in profile from right side, respectively.

Fig. 64. Body of male in dorsal view.

Fig. 65. Palpal patella, tibia, and tarsus.

Fig. 66. Palpal tarsal basal hook.

description given by the author of the species. The form of the abdomen (Fig. 60) should make identification certain. The characteristics of the epigynum are shown in Figures 61-63.

Male allotype. Total length 4.94 mm. Carapace 2.145 mm. long, 1.820 mm. wide opposite interval between second and third coxae where it is widest; without any dorsal swellings; markedly narrowed opposite first coxae (Fig. 64).

Eyes. Eight in two rows as usual; ocular tubercles prominent, especially the laterals; viewed from above, both rows recurved; viewed from in front, anterior row gently recurved, posterior row procurved; central ocular quadrangle wider behind than in front in ratio of 9 : 8, about as long as wide behind. Ratio of eyes AME : ALE : PME : PLE = 5.5 : 4 : 6.5 : 3.5. AME separated from one another by slightly more than their diameter, from ALE by three diameters. PME separated from one another by a little less than their diameter, from PLE by nearly three diameters. Laterals separated from one another by nearly the radius of AME. Height of clypeus equal to about 2.5 times the diameter of AME; clypeus very receding.

Chelicerae. With low basal tubercle in front; unable to observe fang groove and teeth without serious injury to specimen.

Maxillae. Without noteworthy features.

Lip. Wider at base than long in ratio of 4 : 3; transversely and shallowly grooved; with sternal suture procurved.

Sternum. Elongate scutiform; widest between second coxae; longer than wide in ratio of about 3 : 2; considerably and irregularly corrugated; narrowly extended between fourth coxae which are only slightly separated.

Legs. 4123. Width of first patella at "knee" .17328 mm., tibial index of first leg 12. Width of fourth patella at "knee" .15162 mm., tibial index of fourth leg 11.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	1.592	.400	1.085	1.105	.575	4.757
2.	1.495	.390	.845	1.000	.520	4.250
3.	.975	.260	.520	.515	.390	2.660
4.	1.950	.400	.975	.975	.520	4.820
Palp	.400	.110	.110	——	.608	1.228

There is a moderately well developed ventral distal retrolateral hook on the first coxa and the corresponding short prolateral groove and ridge on the second femur. The first two legs are notably spiny, especially on the ventral and prolateral surfaces of the tibiae but the detailed placement seems not to be essential to the adequate description of the allotype. The ventral spines

on the two anterior tibiae are short and robust. Trichobothria are conspicuous on the tibiae.

Palp. Both patella and tibia are short with the latter relatively broad; the shape of the basal tarsal hook is shown in Figure 66; other tarsal features are shown in Figure 65.

Abdomen. With a moderately well developed dorsal scutum: 2.9 mm. long; 1.46 mm. wide in middle; only moderately flattened; other features fairly typical of males of the genus (Fig. 64).

Color in alcohol. Carapace a rich medium brown with fine black dots; legs generally yellowish brown but the first two pairs of femora are darker brown like the carapace. Sternum brown, mottled with black. Abdomen: dorsum with a color pattern essentially as represented in Figure 64. The darkly colored areas are a deep brown, nearly black; the lighter areas are yellowish beneath the scutum but white around the margin; laterally there is a series of seven white elongated spots; the venter is a complex of irregular blackish and brown spots and streaks. The color pattern in mature males is probably quite variable. As already pointed out, one important clue to proper identification of the male is the copious supply of hair in immature specimens.

Type locality. The holotype female came from Guatemala. The hypotype female is from Barro Colorado Island, C. Z., July, 1936. The allotype male is from Barro Colorado Island, C. Z., July, 1934. Two immature males are in my collection from the same locality, June, 1939. Several mature females have been taken on Barro Colorado Island, C. Z., on the following dates: July, 1924 (Banks), July-August, 1936.

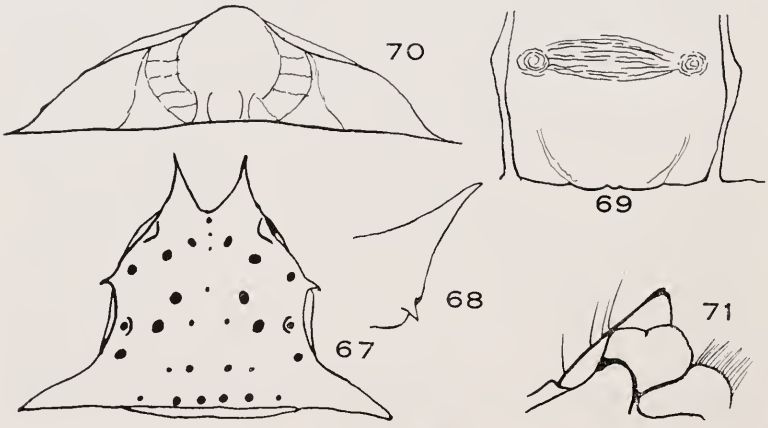
Micrathena gladiola (Walckenaer), 1841

(Figures 67-71)

Acrosoma aculeata C. L. Koch, 1836 (preoccupied)
Plectana gladiola Walckenaer, 1841
A. flaveolum Keyserling, 1892
M. gladiola F. P.-Cambridge, 1904
M. gladiola Petrunkevitch, 1911
M. gladiola Reimoser, 1917
M. flaveola Petrunkevitch, 1925
M. gladiola Roewer, 1942
M. gladiola Bonnet, 1957

In collections made available to me I have found much confusion regarding the identification of this species. I have found

it assigned to other species and other species assigned to it. I am convinced that the group of species to which this belongs should be carefully studied, especially after more careful collecting is done within its area of distribution. In view of the uncertainties surrounding the species, I am relying quite largely upon the descriptions and identifications of both F. P.-Cambridge and Keyserling. The most significant features of the species, taken from a specimen collected at Bugaba, Panama, appear to be the following: The carapace is uniformly convex, not raised behind the median fovea; lateral eyes are on a low tubercle; fang groove with four teeth on promargin and three on retromargin; sternum very convex, raised into a distinct cone; epigynum with features as shown in Figures 69-71 taken from a specimen



External Anatomy of *Micrathena*

Figures 67-71, *M. gladiola*

Fig. 67. Abdomen of female in dorsal view.

Fig. 68. Abdominal spines at posterolateral angle from left side.

Figs. 69-71. Epigynum from below, in posterior view, and in profile from right side, respectively.

studied by F. P.-Cambridge in the British Museum (Natural History); femora finely granulose and with minute setigerous granules in front and beneath; abdominal spines as shown in Figures 67 and 68. The species is quite well known from a few places in Central America, northern South America, and some of the West Indies nearest to South America. The male is still unknown.

Micrathena gracilis (Walckenaer), 1805

(Figures 72-77)

Epeira gracilis Walckenaer, 1805
Plectana gracilis Walckenaer, 1841
Acrosoma matronale C. L. Koch, 1845
E. rugosa Hentz, 1850
A. rugosum Emerton, 1884
Micrathena gracilis Simon, 1895
M. matronalis Simon, 1895
M. gracilis F. P.-Cambridge, 1904
A. gracilis Banks, 1909
M. gracilis Petrunkevitch, 1911
M. gracilis Reimoser, 1917
M. gracilis Chickering, 1931
M. nigrior Chamberlin and Ivie, 1936. New synonymy.
M. gracilis Roewer, 1942
M. gracilis Kraus, 1955
M. gracilis Bonnet, 1957

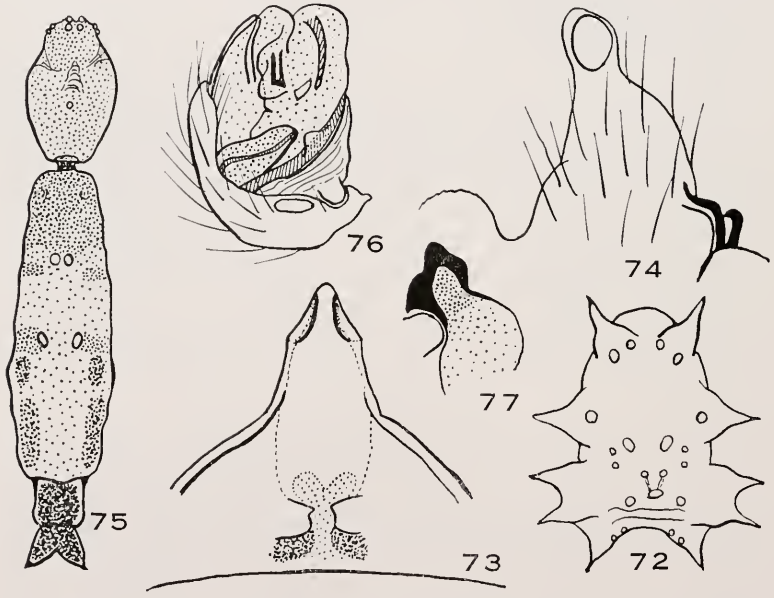
This species is widely distributed from the northern United States through Central America to Brazil. It has been figured and described many times but males remain scarce in collections and there is some evidence of confusion of these with males of other species. Only two males have been found thus far in the collections from Central America. The only record from Panama is that of *M. nigrior* Chamberlin and Ivie, 1936. This is reported to have come from my collection of 1928 but it seems odd that it has not appeared in any of my numerous collections taken since that date.

Female hypotype. Total length 13 mm., including the prominent bases of the chelicerae. Cephalic part of the carapace quite prominent; both lateral ocular tubercles and median ocular tubercles moderately prominent; central ocular quadrangle only slightly wider behind than in front, longer than wide behind in ratio of 8 : 7. Sternum with a pointed tubercle at posterior end. Femora densely granulose with setigerous tubercles. Fang groove with four teeth along the promargin and three along the retromargin. Abdomen very tall; with five pairs of spines (Fig. 72) which should aid greatly in identification. Epigynum more distinctive than usual in the genus (Figs. 73-74).

Male hypotype. Total length 6.11 mm. Abdomen extremely long and slender; strongly chitinized; with a pair of segmental divisions at posterior end, the second of which bears a pair of

stout terminal spines (Fig. 75). The legs appear to lack the modified spines so frequently present in the males of the genus. The first coxa lacks the ventral hook and the second femur also lacks the ridge and groove so frequently present. The chief palpal features are shown in Figures 76-77.

Collection records. The female hypotype is from Patulul, Guatemala, January, 1912 (W. M. Wheeler). The male hypotype is from Orizaba, Mexico, with no date given. Other female specimens studied by me are from: Granada, Nicaragua (C. F. Baker); Polvon, Nicaragua; Tampico, Mexico, 1913 (H. L. Locke); Vera Cruz, Mexico; San Jose, Tamaulipica, Mexico, July, 1930 (Bartlett and Dice); Uricuajo, Costa Rica (Biolley and Tristan). One record only from Panama: *M. nigrior* Chamberlin and Ivie.



External Anatomy of *Micrathena*

Figures 72-77, *M. gracilis*

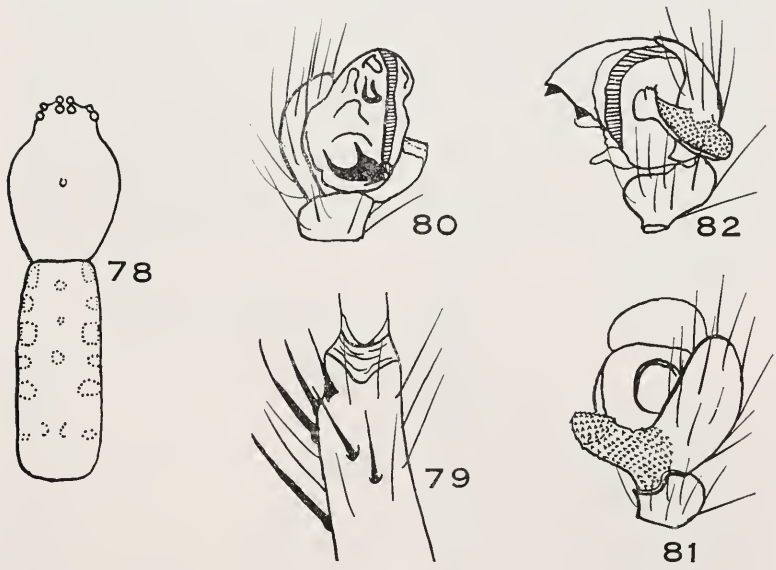
Fig. 72. Abdomen of female, dorsal view.
Figs. 73-74. Epigynum in posterior and profile views, respectively.
Fig. 75. Dorsal view of body of male.
Fig. 76. Left palpal tarsus.
Fig. 77. Palpal tarsal basal hook, more enlarged.

MICRATHENA GRANULATA F. P.-Cambridge, 1904

(Figures 78-82)

M. granulata Petrunkevitch, 1911
M. granulata Reimoser, 1917
M. granulata Roewer, 1942
M. granulata Bonnet, 1957

Male hypotype. Total length 4.16 mm. General form as shown in Figure 78. Legs with ordinary and unnoteworthy spination except for the first femora which, apparently, have a group of clasping spines near the distal end (Fig. 79). The first coxa



External Anatomy of *Micrathena*

Figures 78-82, *M. granulata*

Fig. 78. Dorsal view of body of male.
Fig. 79. Distal end of left first femur; ventral view.
Figs. 80-82. Three different views of left palpal tibia and tarsus showing denticulated basal tarsal hook.

lacks a ventral hook and the second femur lacks the corresponding ridge and groove. Palp: the tarsal hook is very distinctive, being broadly extended, concave, apically recurved, and set with many minute denticles (Figs. 80-82). Color in alcohol: Legs,

cephalothorax, and mouth parts all light reddish brown with variations; abdomen dorsally yellowish with irregular whitish patches (Fig. 78).

For a time it was thought that *M. granulata* was the missing male of *M. catenulata*. Recently a male belonging to this species was found with females clearly belonging to *M. funebris* (Banks) collected on Coronados Island, Gulf of California. At present it would seem that *M. granulata* F. P.-Cambridge could be the missing male for either *M. catenulata* F. P.-Cambridge or *M. funebris* (Banks). On the other hand, perhaps this species belongs with some other of the numerous species known only from females. This condition again emphasizes the need for careful collecting and close observation over the whole area occupied by this genus.

Collection records. F. P.-Cambridge had the species only from Teapa, Mexico. The male hypotype is from Chiapas, Escuintla, Mexico with no date of collection given. I have a second specimen taken with the hypotype and another from Coronados Island, Gulf of California, May 18, 1921. These three are all in the collection of the Museum of Comparative Zoology at Harvard College.

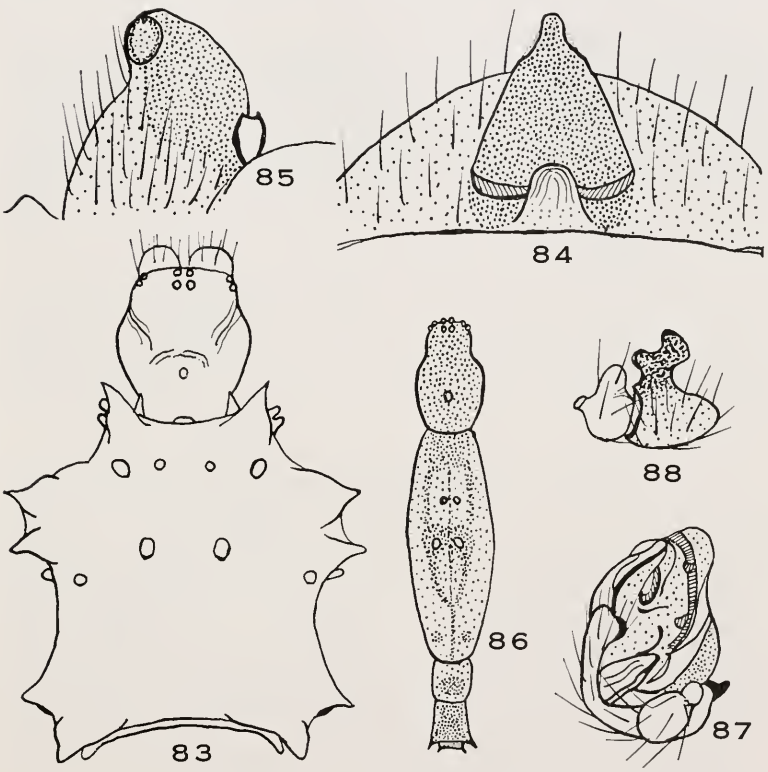
Micrathena horrida (Taczanowski), 1873

(Figures 83-88)

Acrosoma horrida Taczanowski, 1873
A. mammillata Butler, 1873
A. longicauda Keyserling, 1892. New synonymy.
M. mammillata F. P.-Cambridge, 1904
A. longicauda O. P.-Cambridge, 1890. New synonymy.
M. longicauda F. P.-Cambridge, 1904. New synonymy.
A. mammillata Banks, 1909
M. horrida Petrunkevitch, 1910
M. horrida Petrunkevitch, 1911
M. mammillata Petrunkevitch, 1911
M. longicauda Petrunkevitch, 1911. New synonymy.
M. horrida Reimoser, 1917
M. longicauda Reimoser, 1917. New synonymy.
M. horrida Petrunkevitch, 1925
M. longicauda Petrunkevitch, 1925. New synonymy.
M. longicauda Banks, 1929. New synonymy.
A. mammillata Banks, 1929
M. mammillata Bryant, 1940
M. horrida Roewer, 1942

M. longicauda Roewer, 1942. New synonymy.
M. horrida Bonnet, 1957
M. longicauda Bonnet, 1957. New synonymy.

Until recently it has seemed unsafe to American araneologists to synonymize *M. mammillata* (Butler) with *M. horrida* (Taczanowski). It now seems to me that the synonymy as indicated is



External Anatomy of *Micrathena*

Figures 83-88, *M. horrida*

Fig. 83. Dorsal view of body of female.
Figs. 84-85. Epigynum in posterior view, and in profile, right side, respectively.
Fig. 86. Dorsal view of body of male.
Fig. 87. Left palpal tibia and tarsus of male.
Fig. 88. Male palpal tibia and basal tarsal hook to show form of latter.

fully justified. F. P.-Cambridge suggested that *M. longicauda* (O. P.-Cambridge) might be the male of *M. mammillata* (Butler). Banks (1929) was quite convinced that this was so but he continued to list them separately. Miss Bryant (1940) recognized the male of *M. mammillata* but did not synonymize it with *M. longicauda*. The species appears to be closely related to *M. gracilis* (Walck.); this conclusion is based upon a comparison of both sexes of both species.

Female hypotype. Total length 8.9 mm., including the prominent bases of the chelicerae. Very strongly chitinized. Carapace with raised cephalic part; only slightly raised behind median fovea. Sternum convex but without a posterior tubercle as seen in *M. gracilis*. The femora are excessively provided with setigerous tubercles. Abdomen: with seven pairs of marginal spines the first of which extends from the anterior margin over the posterior lateral corners of the carapace (Fig. 83); there are also numerous lateral tubercles beneath the marginal spines (five on each side in the hypotype) subject to considerable variation among the many specimens available; the epigynum is strongly tubercular (Figs. 84-85); there is also a prominent, median, chitinized tubercle just posterior to the cone surrounding the spinnerets.

Male hypotype. Total length 4.85 mm. Very long and slender; strongly chitinized (Fig. 86). Abdomen with a trilobate posterior termination; the trilobate termination bears four small but definite spines. Legs without especially modified spines; femora one and two with numerous small setigerous tubercles; patellae one and two quite dilate on retromargin; coxa one without any ventral hook and femur two without the corresponding ridge and groove. Features of the palp with tarsal hook shown in Figures 87-88. The shape of the abdomen and the palpal features furnish the best means of identification of the male of the species.

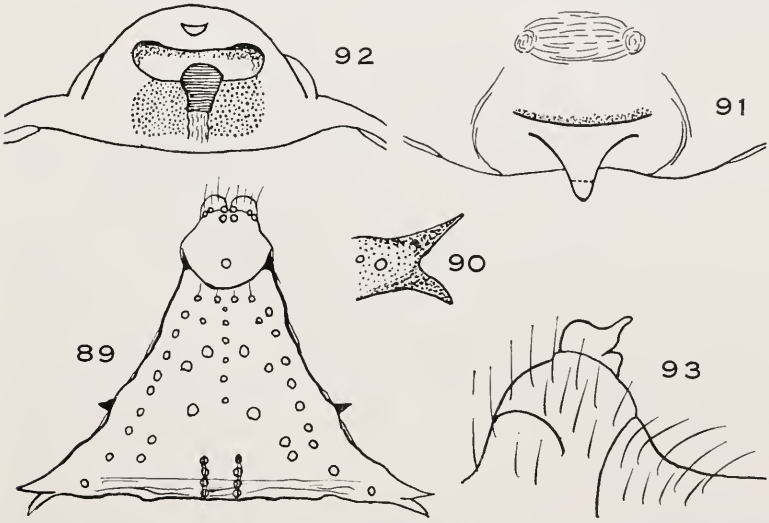
Collection records. Male and female hypotypes are from Barro Colorado Island, C. Z., July and August, 1950, respectively. The species is widely distributed from the southern United States through Central America to several countries in northern South America and the West Indies. It occurs in my collections from many localities in Panama and is abundant on Barro Colorado Island.

Micrathena inaequalis F. P.-Cambridge, 1904

(Figures 89-93)

Acrosoma inaequalis Banks, 1909
M. inaequalis Petrunkevitch, 1911
M. inaequalis Reimoser, 1917
M. inaequalis Chickering, 1936
M. inaequalis Roewer, 1942
M. inaequalis Bonnet, 1957

F. P.-Cambridge (1904) had this species from Costa Rica and Guatemala. Banks (1909) had it from Costa Rica. I reported it from Panama in 1936 but at that time the specimens in my possession were all immature and may have been wrongly identified. Now I can definitely record the species from the highlands of western Panama.



External Anatomy of *Micrathena*

Figures 89-93, *M. inaequalis*

Fig. 89. Dorsal view of body of female.
Fig. 90. Posterolateral abdominal spines; posterior view.
Figs. 91-93. Epigynum from below, in posterior view, and in profile from right side, respectively.

Hypotype female. Total length 7.8 mm. Carapace raised both before and behind the median fovea. Sternum moderately convex; with a series of low marginal tubercles. Abdomen: there

is a pair of sharply pointed spines reaching far over the carapace; there is also a pair of short marginal spines somewhat behind the middle; the abdomen extends far laterally at the posterior border and there terminates in a pair of spines on each side (Figs. 89-90). These eight spines seem to be typical of the species but small lateral marginal spines may also occur on some specimens. The degree to which the large posterior lateral spines are separated is also, apparently, at least somewhat variable in the general population. Characteristics of the epigynum are shown in Figures 91-93.

Collection records. In addition to the earlier records of the species from Costa Rica and Guatemala I can now add the following from Panama: El Valle, July, 1936; Boquete, Chiriqui, July, 1939; El Volcan, Chiriqui, August, 1950. The hypotype female is from Boquete, July, 1939. The male is unknown.

Micrathena insolita sp. nov.

(Figures 94-98)

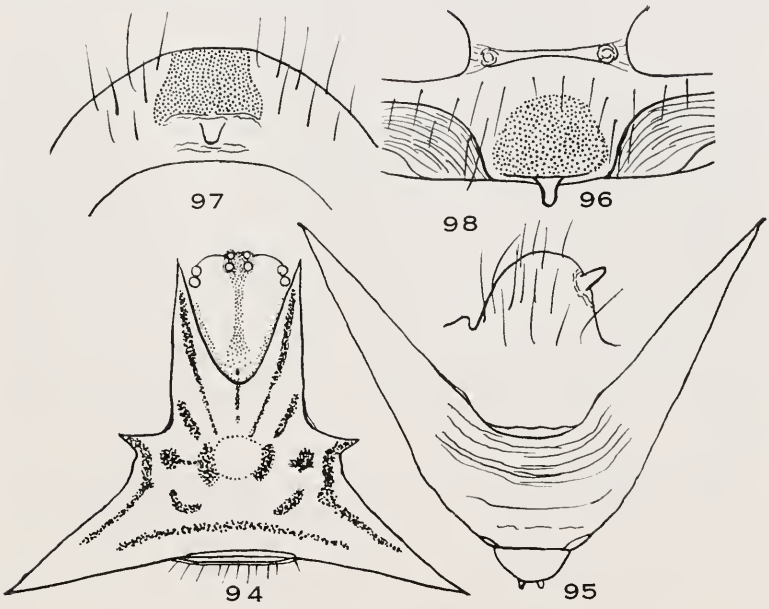
Apparently the holotype had recently completed its last moult and was not yet well chitinized. It is, however, in good condition for describing.

Female holotype. Total length 4.55 mm. Carapace largely covered by the anterior marginal abdominal spines and projecting anterior end of the abdomen itself; about 2.08 mm. long and about 1.625 mm. wide opposite interval between second and third coxae where it is widest; median thoracic fovea obscure; regularly and gently arched dorsally from PME to posterior declivity with no marked gibbosity as in many species in the genus.

Eyes. Eight in two rows as usual: viewed from above, both rows recurved; viewed from in front, both rows procurved, posterior row strongly so; central ocular quadrangle wider behind than in front in ratio of about 3 : 2, wider behind than long in ratio of about 18 : 13. Ratio of eyes AME : ALE : PME : PLE = 7 : 7 : 8 : 7 (laterals somewhat oval). AME separated from one another by a little more than 1.5 times their diameter, from ALE by nearly six times their diameter. PME separated from one another by slightly more than 2.5 times their diameter, from PLE by about 5 times their diameter. Laterals separated from one another by about the radius of ALE. Height of clypeus equal to 1.5 times the diameter of AME.

Chelicerae. Parallel, moderately robust; as usual in the genus. Unable to see fang groove because of fragility of the holotype.

Maxillae and Lip. Apparently as usual in the genus and without noteworthy features.



External Anatomy of *Micrathena*

Figures 94-98, *M. insolita*

Fig. 94. Dorsal view of body of female.

Fig. 95. Posterior end of abdomen; seen from posterior surface.

Figs. 96-98. Epigynum from below, from a somewhat posterior view, and in profile from right side, respectively.

Sternum. Quite convex; without tubercles; posterior coxae separated by about half their width.

Legs. 4123. Width of first patella at "knee" .2274 mm., tibial index of first leg 12. Width of fourth patella at "knee" .2373 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	1.690	.715	1.170	1.040	.617	5.232
2.	1.660	.715	1.040	.975	.520	4.910
3.	1.170	.650	.530	.747	.520	3.617
4.	2.145	.650	1.170	1.202	.617	5.784

Legs with few spines; details of spination seem to be unnoteworthy.

Abdomen. Measured with anterior and posterior spines, as long as entire body. Three pairs of spines as indicated in Figures 94-95. Perhaps the most striking feature is the extreme extension of the anterior pair of spines.

Epigynum. Features of this organ essentially as shown in Figures 96-98. This organ lies so close to the chitinized cone surrounding the spinnerets that it is impossible to view it from the posterior surface in the usual manner.

Color in alcohol. Legs generally yellowish; first two pairs with a dorsal brown stripe on femora, patellae, tibiae, and metatarsi with the tarsi entirely brown; second two pairs of legs similarly colored except the brown stripe is changed to a large spot of irregular shape. Carapace yellowish in anterior half with brown dots and a narrow brown median stripe; posterior half with brown dots closely crowded together. Abdomen: dusky yellowish dorsally with black stripes and spots as suggested in Figure 94; posterior and lateral surfaces yellowish with irregular black stripes.

Type locality. Female holotype from Porto Bello, Panama, August, 1936. There are no paratypes and the male is unknown.

Micrathena macfarlanei sp. nov.

(Figures 99-102)

Female holotype. Total length from AME to middle of posterior margin of abdomen 11.05 mm. Carapace about 4 mm. long (considerably overlapped by abdomen), 3.185 mm. wide opposite posterior border of second coxae where it is widest; quite strongly gibbous just posterior to well defined median fovea; with paired dorsolateral foveae very faintly indicated; gently raised just posterior to PME.

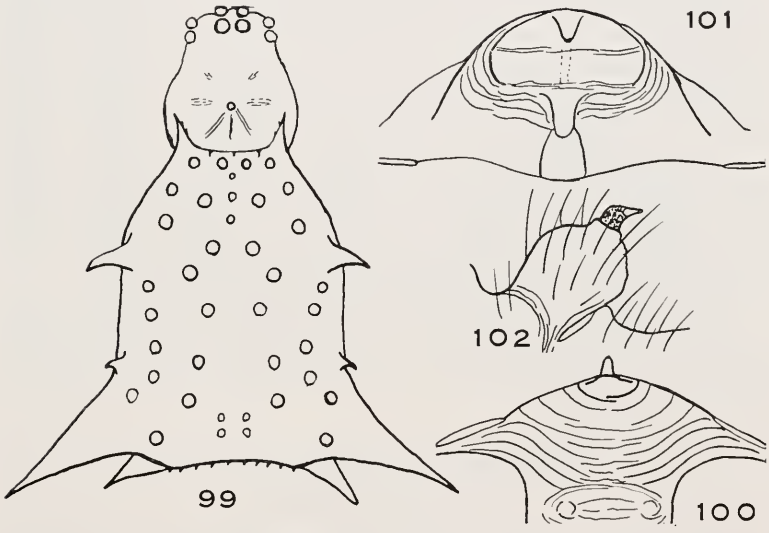
Eyes. Eight in two rows as usual; viewed from above, both rows moderately recurved; viewed from in front, anterior row slightly recurved, posterior row slightly procurved, all measured by centers. Central ocular quadrangle wider behind than in front in ratio of about 19 : 17; wider behind than long in ratio of about 19 : 16. Ratio of eyes AME : ALE : PME : PLE = 6.5 : 4.5 : 7 : 4.5. AME separated from one another by ten-thirteenths of their diameter, from ALE by about 4 times their diameter. PME separated from one another by slightly more than their diameter, from PLE by four times their diameter.

Laterals separated from one another by slightly less than one-fourth of the diameter of one of them. Height of clypeus equal to slightly more than the diameter of AME.

Chelicerae. Robust; gibbous in front near base. Promargin of fang groove with four teeth, retromargin with three robust teeth.

Maxillae and *Lip.* Typical of females of the genus; details regarded as unnoteworthy.

Sternum. Sternal suture procurved; anterolateral tubercles moderately well developed, others hardly tubercular, more rounded ridges; continuous posteriorly with a sclerite extending between fourth coxae which are separated by two-fifths of their width.



External Anatomy of *Micrathena*

Figures 99-102, *M. macfarlanei*

Fig. 99. Dorsal view of body of female.

Figs. 100-102. Epigynum from below, in posterior view, and in profile from right side, respectively.

Legs. 4123. Width of first patella at "knee" .520 mm., tibial index of first leg 10. Width of fourth patella at "knee" .520 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	5.005	1.365	3.575	3.575	1.105	14.625
2.	4.615	1.300	3.055	3.120	.975	13.065
3.	2.730	.925	1.625	1.480	.845	7.605
4.	6.500	1.240	3.315	4.355	1.235	16.645

Setigerous tubercles numerous on legs; true spines few; first femora with a series of six or seven very short prolateral spines.

Abdomen. Plump and full; somewhat convex dorsally; general form and five pairs of spines as shown in Figure 99.

Epigynum. Essentially as shown in Figures 100-102.

Color in alcohol. Legs with varying shades of reddish brown. Carapace with a narrow, median, dusky brown stripe from between PME to near median fovea; with a broad, broken, dusky brown, dorsolateral stripe on each side leaving the margins yellowish. Sternum dark brown. Lip dark brown, nearly black, with a yellowish tip. Maxillae dark brown with anterior and median margins yellowish. Chelicerae: fang and tips of basal segments dark brown, elsewhere yellowish. Abdomen: dorsal region almost white with black "punctures"; second, fourth, and fifth spines reddish at bases with more or less black striping; lateral sides and venter a variegated black and yellowish.

Type locality. Female holotype from Barro Colorado Island, C. Z., August, 1934; one mature paratype female and several immature females from the same locality, July, 1936 and June, 1939.

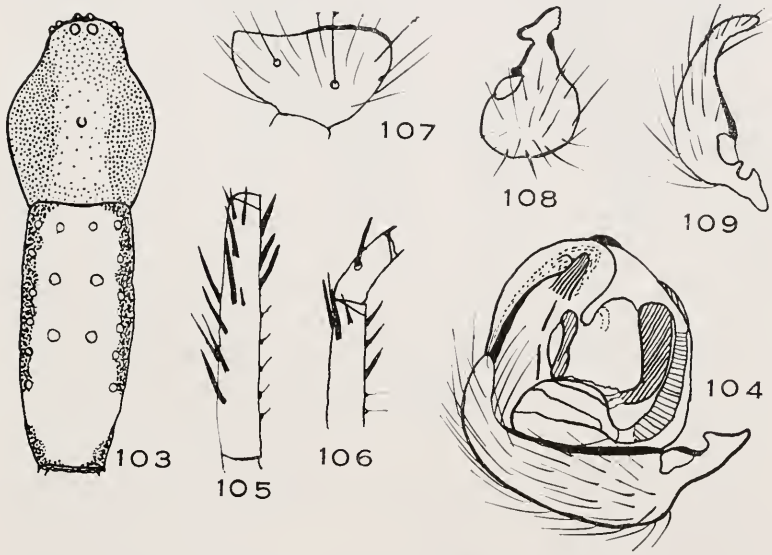
Micrathena macilenta sp. nov.

(Figures 103-109)

Note: The two specimens treated under the name *M. macilenta* sp. nov. were formerly believed to belong to the species named *M. parallela* (O. P.-Cambridge) but a careful comparison with the type of the latter species in the British Museum (Natural History) has shown this to be an error and so they must be regarded as representing a species new to science. One is selected, therefore, as the holotype and described in accord with my usual procedure.

Male holotype. Total length 3.95 mm. Carapace 1.76 mm. long; somewhat overlapped by abdomen; 1.30 mm. wide slightly behind second coxae where it is widest; .66 mm. tall just behind well developed median fovea where it is tallest.

Eyes. Eight in two rows as usual; ocular tubercles only moderately developed; viewed from above, both rows strongly recurved; viewed from in front, anterior row slightly procurved, posterior row strongly procurved, all measured by centers. Central ocular quadrangle wider behind than in front in ratio of 11 : 9, wider behind than long in ratio of 22 : 19. Ratio of eyes AME : ALE : PME : PLE = 7 : 6 : 8 : 5.5. AME separated from one another by slightly less than their diameter,



External Anatomy of *Micrathena*

Figures 103-109, *M. macilenta*

Fig. 103. Dorsal view of body of male.
Fig. 104. Left palpal tarsus.
Fig. 105. Left first femur; prolateral view.
Fig. 106. Distal end of left second femur and patella; prolateral view.
Fig. 107. Dorsal view of left palpal tibia.
Figs. 108-109. Two views of left palpal cymbium and basal tarsal hook.

from ALE by nearly two and one-third times their diameter. PME separated from one another by their diameter, from PLE by two and one-half times their diameter. Laterals separated from one another only by a well defined line. Height of clypeus equal to about one and one-fifth times the diameter of AME.

Chelicerae, *Maxillae*, and *Lip*. All apparently quite typical of males of the genus. Teeth along fang groove not observed because of fragility of the holotype.

Sternum. Only slightly convex; slightly rugulose; without definite tubercles; continued as a narrow sclerite between coxae laterally and as a fairly broad, thin sclerite between fourth coxae which are separated by about one-third of their width.

Legs. 1423. Width of first patella at "knee" .17328 mm., tibial index of first leg 11. Width of fourth patella at "knee" .15162 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	1.520	.528	1.056	1.000	.484	4.588
2.	1.300	.440	.814	.770	.440	3.764
3.	.704	.290	.396	.418	.352	2.160
4.	1.540	.352	.814	.980	.418	4.104
Palp	.308	.141	.141	——	.572	1.162

The ventral, distal, retrolateral hook on first coxa and the corresponding ridge and groove on the proximal prolateral surface of the second femur are moderately well developed. There are numerous spines on legs; those with most significance appear to be on the first and second femora essentially as shown in Figures 105-106.

Palp. General features as shown in Figures 104, 107-109. Resembles that of *M. parallela* (O. P.-Cambridge) with which the species was formerly confused.

Abdomen. Much flattened dorsoventrally; the only evidence of suppressed spines shows at posterior end where two pairs of small tubercles occur; other features as usual in males of the genus (Fig. 103).

Color in alcohol. Legs and mouth parts variable shades of yellowish; not distinctive. Carapace yellowish in the center, brownish elsewhere. Abdomen: dorsum nearly white throughout center with irregular black marginal stripes as shown in Figure 103; venter dusty yellowish with gray patches in regions of booklungs. Paratype follows the color pattern of the holotype very closely.

Type locality. Male holotype from Barro Colorado Island, C. Z., July, 1934; one paratype male from the same locality, August, 1950, and one taken in December, 1957. The female is unknown.

Micrathena militaris (Fabricius), 1775

Aranea militaris Fabricius, 1775
A. militaris Olivier, 1789
Plectana militaris Walckenaer, 1841
Acrosoma militaris Butler, 1873
A. militare Banks, 1898
M. militaris Petrunkevitch, 1911
M. militaris Reimoser, 1917
M. militaris Petrunkevitch, 1930
M. militaris Roewer, 1942
M. militaris Bonnet, 1957

Banks (1898), with some uncertainty, reported this species from Margarita Island, Lower California. The single specimen now in the Museum of Comparative Zoology from Margarita Island and labelled *M. militaris* (Fabr.) is a specimen of *M. sexspinosa* (Hahn). Another specimen from Western Mexico with a similar label is a female of *M. sagittata* (Walck.). I am assuming, therefore, that *M. militaris* (Fabr.) has not yet been found in Central America.

Micrathena mitrata (Hentz), 1850

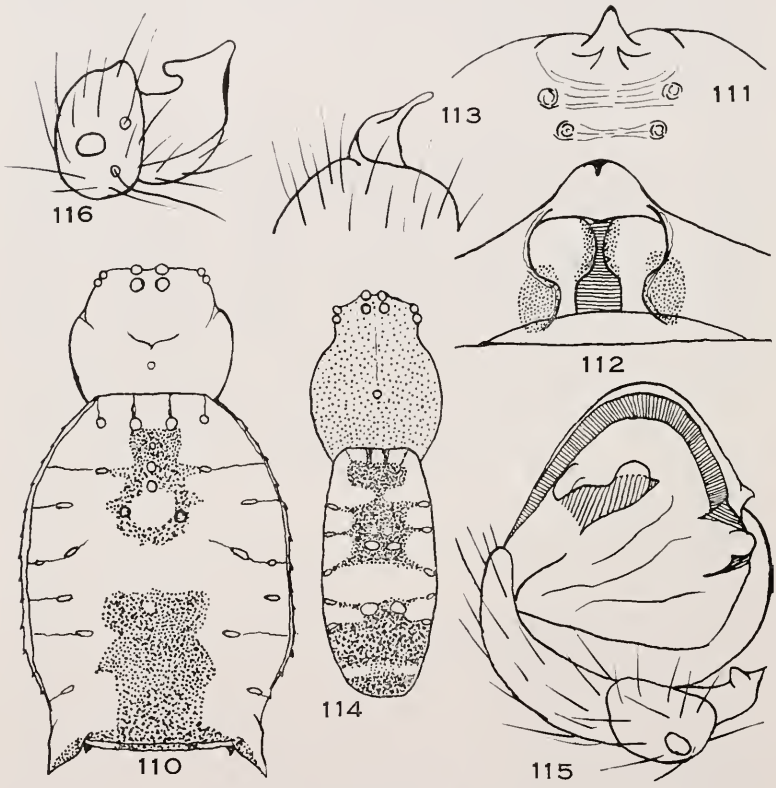
(Figures 110-116)

Acrosoma mitrata Hentz, 1850
A. mitrata Emerton, 1884
A. reduvianum McCook, 1893
A. mitrata Banks, 1898
A. mitrata Emerton, 1902
M. mitrata F. P.-Cambridge, 1904
M. reduviana Petrunkevitch, 1911
M. mitrata Reimoser, 1917
M. mitrata Roewer, 1942
M. mitrata Kaston, 1948
M. mitrata Levi, 1954
M. mitrata Bonnet, 1957

The female of this species is well known from many localities in the United States. It has also been reported from Mexico and, doubtfully, from Cuba (Franganillo). The male, apparently, has not been carefully studied and appears to be scarce in collections. In general, the specimens from the United States studied by me agree well with those from Mexico in the British Museum (Natural History). The hypotypes have been selected from collections made in Canton, North Carolina, and kept in the Museum

of Comparative Zoology. There is no date of collection given but the specimens have been in preservation a long time.

Female hypotype. Total length 4.55 mm. Probably the best means of identification is the presence of two pairs of posterolateral abdominal spines (Fig. 110). Prominent spines are lacking elsewhere but there are many small lateral spinules usually



External Anatomy of *Micrathena*

Figures 110-116, *M. mitrata*

Fig. 110. Dorsal view of body of female.

Figs. 111-113. Epigynum from below, in posterior view, and in profile from right side, respectively.

Fig. 114. Dorsal view of body of male.

Fig. 115. Left palpal tarsus of male.

Fig. 116. Palpal tibia and basal tarsal hook of male, more enlarged.

not mentioned in descriptions. The lateral spinules appear to be less evident in the specimens from Mexico than among those from the United States which I have had an opportunity to study. In some of the specimens in the British Museum (Natural History) from Mexico there appeared to be a tendency for the anterolateral corners of the abdomen to be somewhat extended. The epigynum is obscurely distinctive (Figs. 111-113).

Male hypotype. Total length 3.25 mm. Abdominal spines are completely suppressed in the male (Fig. 114). Features of the palp are difficult to determine and present in drawings because of long preservation, minute size, and some deterioration, but Figures 115-116 are believed to give the most important characteristics. The coxal hook and corresponding femoral groove and ridge are poorly developed.

Micrathena mirifica sp. nov.

(Figures 117-121)

Male holotype. Total length 4.03 mm. Carapace 1.69 mm. long; 1.495 mm. wide opposite interval between second and third coxae where it is widest; considerably overlapped by anterior end of abdomen; median fovea only slightly behind middle; median region nearly level from PME to posterior declivity; with lateral margins regularly rounded to cephalic region (Fig. 117).

Eyes. Eight in two rows as usual; viewed from above, both rows recurved; viewed from in front, anterior row nearly straight, posterior row procurved, all measured by centers. Central ocular quadrangle only slightly wider behind than in front, slightly longer than wide behind. Ratio of eyes AME : ALE : PME : PLE = 7 : 5 : 7 : 5 (laterals somewhat angular). AME separated from one another by slightly less than their diameter, from ALE by about 2.5 times their diameter. PME separated from one another by slightly less than their diameter, from PLE by about three times their diameter. Laterals separated from one another by about one-third of their diameter. Height of clypeus equal to about 1.5 times the diameter of AME. Clypeus quite receding. Median ocular tubercle quite prominent; lateral ocular tubercles moderately prominent.

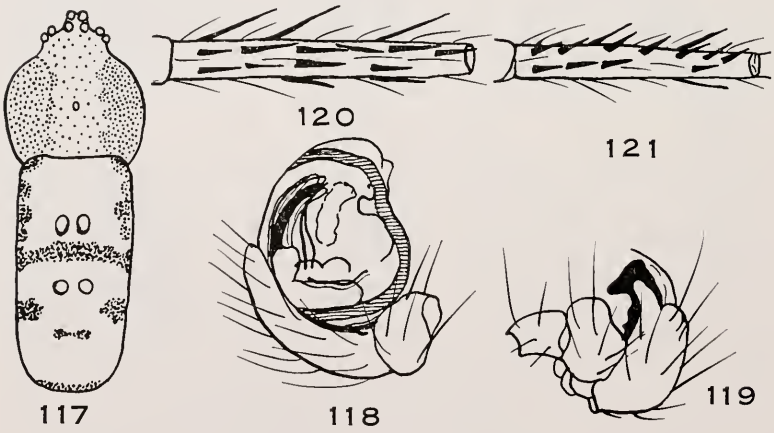
Chelicerae, *Maxillae*, and *Lip.* Quite as usual in males of the genus and without noteworthy features.

Sternum. Nearly flat; without noteworthy features. Pedicel with pointed tubercle projecting forward toward posterior end of sternum. Posterior coxae separated by a little more than half their width.

Legs. 1423. Width of first patella at "knee" .166 mm., tibial index of first leg 10. Width of fourth patella at "knee" .154 mm., tibial index of fourth leg 14.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	1.852	.540	1.040	1.040	.525	4.997
2.	1.430	.410	.715	.780	.500	3.835
3.	.760	.300	.455	.400	.325	2.240
4.	1.625	.390	.745	.845	.455	4.060
Palp	.325	.152	.162	——	.638	1.277

Spines: first femur without special clasping spines; first tibia with long, robust, prolateral, and ventral spines as shown in Figure 120; second tibia with short, robust, prolateral, and ventral spines as shown in Figure 121. Without coxal hook and femoral ridge and groove.



External Anatomy of *Micrathena*

Figures 117-121, *M. mirifica*

Fig. 117. Dorsal view of body of male.
Fig. 118. Left palpal tibia and tarsus.
Fig. 119. Left palpal patella, tibia, and basal tarsal hook.
Figs. 120-121. Left first and second tibiae, respectively; ventral view.

Palp. The tibia is simple, without spines or special modifications. Other palpal features, including tarsal hook, shown in Figures 118-119.

Abdomen. Wholly without spines; considerably flattened dorsoventrally; with form as shown in Figure 117.

Color in alcohol. Legs yellowish brown above with small dusky patches; lighter below. Carapace light brown in center with broad, darker brown lateral stripes. Abdomen nearly white dorsally with black markings as suggested in Figure 117. Sternum yellowish with a large black spot in posterior half. Color pattern of paratypes like that of holotype.

Type locality. Male holotype and one paratype from Barro Colorado Island, C. Z., July, 1950; one additional paratype from the same locality, July, 1939.

Micrathena modica sp. nov.

(Figures 122-126)

Male holotype. Total length 4.29 mm. Carapace 1.625 mm. long; 1.43 mm. wide just behind second coxae where it is widest; thoracic part regularly rounded laterally; .585 mm. tall just behind the moderately well marked central fovea where it is tallest; considerably overlapped by anterior border of abdomen.

Eyes. Eight in two rows as usual; lateral ocular tubercles moderately well developed; central ocular tubercle hardly existent. Viewed from above, both rows rather strongly recurved; viewed from in front, anterior row gently recurved, posterior row clearly procurved, all measured by centers. Central ocular quadrangle only slightly wider behind than in front, almost exactly as long as wide behind. Ratio of eyes AME : ALE : PME : PLE = 8 : 6 : 8.5 : 6. AME separated from one another by nearly their diameter, from ALE by about three-halves of their diameter. PME separated from one another by about their diameter, from PLE by about twice their diameter. Laterals separated from one another by a broad line. Height of clypeus equal to about nine-eighths of the diameter of AME.

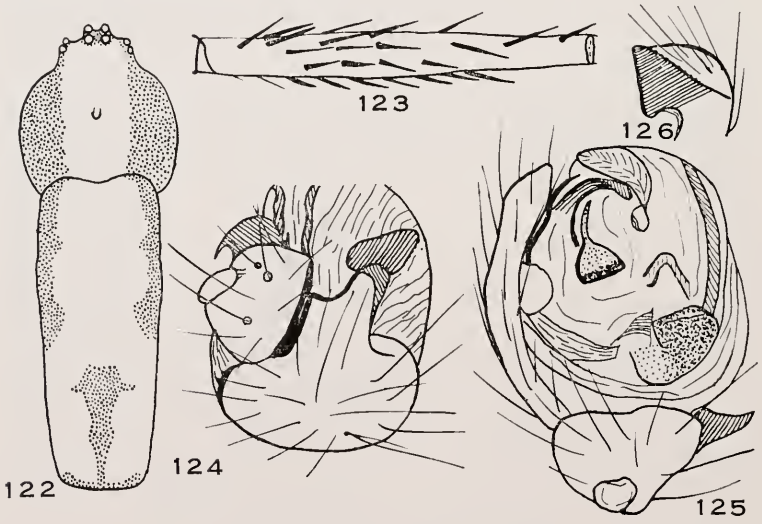
Chelicerae, *Maxillae*, and *Lip.* Apparently quite typical of males in the genus. Teeth along the fang groove not observed because of fragility of the holotype.

Sternum. Only slightly convex; tubercles almost completely suppressed; posterior end extended between fourth coxae which are separated by about two-thirds of their width.

Legs. 1243. Width of the first patella at "knee" .19494 mm., tibial index of first leg 9. Width of fourth patella at "knee" .15162 mm., tibial index of fourth leg 9.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.470	.600	1.690	1.625	.650	7.035
2.	2.085	.575	1.320	1.365	.520	5.865
3.	1.170	.357	.585	.720	.390	3.222
4.	1.975	.455	1.170	1.276	.540	5.416
Palp	.286	.132	.154	——	.528	1.100

The ventral distal retrolateral hook on first coxa and the corresponding proximal prolateral groove and ridge on the second femur are all lacking in this species. The legs are all quite spiny but the modified spines appear to be most important on the first femur (Fig. 123). Probably a considerable degree of variation in the spination will be noted when a series of these males is available for study.



External Anatomy of *Micrathena*

Figures 122-126, *M. modica*

Fig. 122. Dorsal view of body of male.
Fig. 123. Left first femur; ventral view.
Fig. 124. Left palpal tibia and base of tarsus with tarsal hook.
Fig. 125. Left palpal tibia and tarsus.
Fig. 126. Another view of basal tarsal hook.

Palp. General features shown in Figures 124-126. The basal tarsal hook resembles those of certain other species but is also somewhat distinctive. The tibia is conservative and without special features.

Abdomen. General features as shown in Figure 122. Much flattened dorsoventrally; with no indication of suppressed spines.

Color in alcohol. Legs and mouth parts in varying shades of brownish and yellowish colors; details regarded as unessential. Carapace with a yellowish brown central stripe and a broad dusky brown stripe on each side as indicated by stippling in Figure 122. Abdomen: with many white subchitinous flecks on dorsum together with dark markings also as indicated in Figure 122.

Type locality. Male holotype is from Summit, Canal Zone, July, 1950. One paratype male from Barro Colorado Island, C. Z., July, 1950; one immature male from El Volcan, Chiriqui, August, 1950 showing short spines at posterior end of abdomen. The female is unknown.

Micrathena molesta sp. nov.

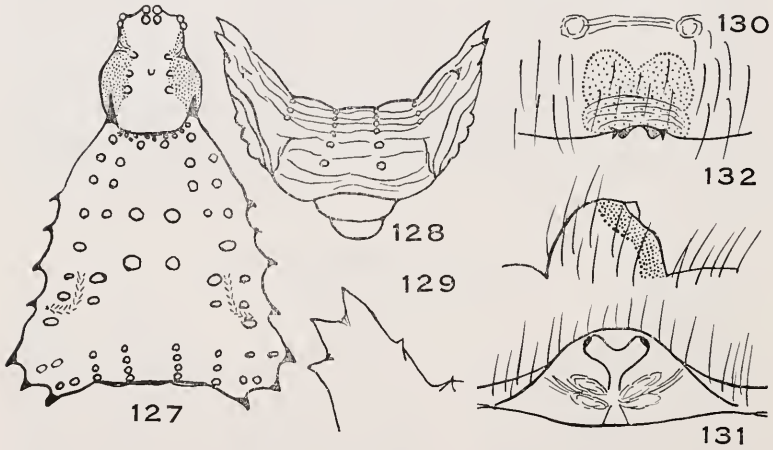
(Figures 127-132)

Note: The holotype specimen deseribed below was found in the Nathan Banks collection in the Museum of Comparative Zoology. It was filed with two other specimens and labelled *M. triserrata* F. P.-Cambridge. I have carefully compared the holotype with those specimens assigned to *M. triserrata* F. P.-Cambridge in the British Museum (Natural History) and have been compelled to decide that they do not belong together. For this reason, but somewhat hesitantly, I have been compelled to consider the species new to science and, therefore, I am describing the holotype in accord with my usual procedure.

Female holotype. Total length 6.825 mm. Carapace about 2.21 mm. long; 1.82 mm. wide opposite the interval between second and third coxae where it is widest; 1.40 mm. tall at level of marked gibbosity just behind the central fovea which is well defined; with three pairs of dorsolateral foveae also well defined (Fig. 127).

Eyes. Eight in two rows as usual; viewed from above, posterior row moderately recurved, anterior row strongly so. Viewed from in front, anterior row gently recurved, posterior row gently procurved, all measured by centers. Central ocular quadrangle

wider behind than in front in ratio of about 6 : 5, wider behind than long in ratio of 15 : 14. Ratio of eyes AME : ALE : PME : PLE = 9.5 : 7.5 : 11 : 6. AME separated from one another by a little less than their diameter, from ALE by a little less than 2.5 times their diameter. PME separated from one another by a little more than their diameter, from PLE by about five-thirds of their diameter. Laterals separated from one another by about one-fourth the diameter of PLE (a deformity has removed the PLE far away from the ALE on the right side). Height of clypeus equal to about the radius of AME.



External Anatomy of *Micrathena*

Figures 127-132, *M. molesta*

Fig. 127. Dorsal view of body of female.

Fig. 128. Posterior end of abdomen from behind.

Fig. 129. Right lateral view of posterolateral corner of abdomen.

Figs. 130-132. Epigynum from below, in posterior view, and in profile from right side, respectively.

Chelicerae, Maxillae, and *Lip.* All apparently quite typical of the genus and with details regarded as unnoteworthy.

Sternum. A simple scutiform; sternal suture nearly straight; anterolateral tubercles moderately developed, others hardly indicated; not continued between fourth coxae which are separated by about one-third of their width.

Legs. 4123. Width of first patella at "knee" .22743 mm., tibial index of first leg 11. Width of fourth patella at "knee" .23826 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.080	.725	1.430	1.105	.630	5.970
2.	1.950	.655	1.190	1.040	.585	5.420
3.	1.300	.425	.780	.650	.390	3.545
4.	2.470	.640	1.430	1.495	.630	6.665

With few spines on legs; exact number and placement not regarded as essential for adequate description; with many setigerous tubercles.

Abdomen. General form as shown in Figures 127-129. The holotype has eight pairs of spines as shown; one of the paratypes has the same number but the other has the three small lateral spines on each side represented only by tubercles.

Epigynum. Essentially as shown in Figures 130-132. One paratype agrees well with the holotype in this respect but the other does not, perhaps because of immaturity.

Color in alcohol. Carapace a reddish brown with lateral sides dusky as indicated by stippling in Figure 127. Sternum a lighter reddish brown. Legs and mouth parts with varying shades of reddish brown. Abdomen: dorsum almost entirely yellowish with small white subchitinous flecks; the numerous "punctures" are reddish brown.

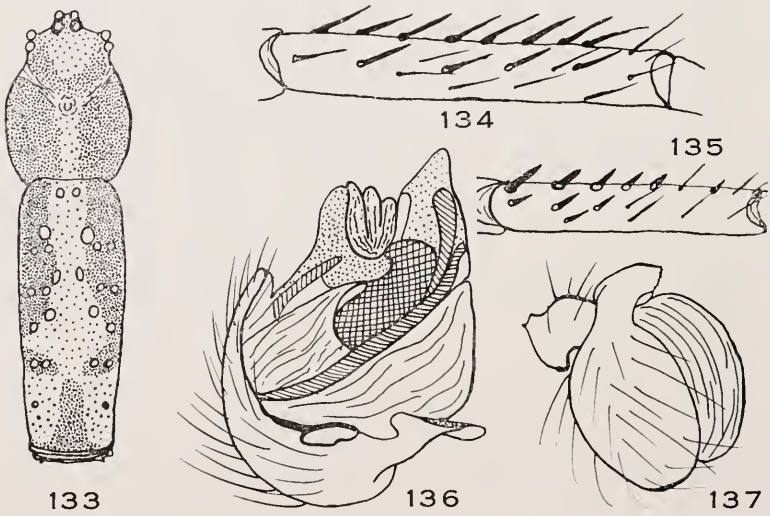
Type locality. Holotype female together with two paratype females from Tablazo, Costa Rica. Apparently collected by Prof. Tristan during the early part of the present century and reported as *M. triserrata* F. P.-Cambridge (Banks, 1909). The male is unknown.

Micrathena parallela (O. P.-Cambridge), 1890

(Figures 133-137)

Acrosoma parallelum O. P.-Cambridge, 1890
A. parallelum Keyserling, 1892
M. parallela F. P.-Cambridge, 1904
M. parallela Petrunkevitch, 1911
M. parallela Reimoser, 1917
M. parallela Petrunkevitch, 1925
M. parallela Roewer, 1942
M. parallela Bonnet, 1957

The Pickard-Cambridges (1890, 1904) reported this species from Panama and Guatemala. Keyserling (1892) mentions having numerous specimens from Guatemala. The species has not yet appeared in my collections and my only opportunity to study it came during my period of work in the British Museum (Natural History) in the summer of 1958. The type material now consists of parts of four specimens from which the following facts have been taken. Apparently there are no highly modified femoral spines in this species such as frequently occur in males of the genus; some variation in respect to tibial spines has been noted among the available specimens but the ventral spines on the first and second tibiae are probably fairly typical (Figs. 134-135); there is some discoloration from long preservation but in



External Anatomy of *Micrathena*

Figures 133-137, *M. parallela*

Fig. 133. Dorsal view of body of male.
Fig. 134. Ventral spines of first tibia.
Fig. 135. Ventral spines of second tibia.
Fig. 136. Palpal tarsus.
Fig. 137. Base of palpal tarsus with another view of basal tarsal hook.

general the color is a dull reddish brown with carapace lighter in head region and along central region; abdomen is irregularly

yellowish through the center and much darker on lateral sides; the body is much flattened dorsoventrally with lateral sides nearly parallel; the first coxa has the ventral hook well developed and the second femur is provided with the corresponding groove and ridge; Figures 136-137 show the most important features of the palpal basal tarsal hook and other parts of the palpal tarsus. The female is unknown.

Micrathena patruelis (C. L. Koch), 1839

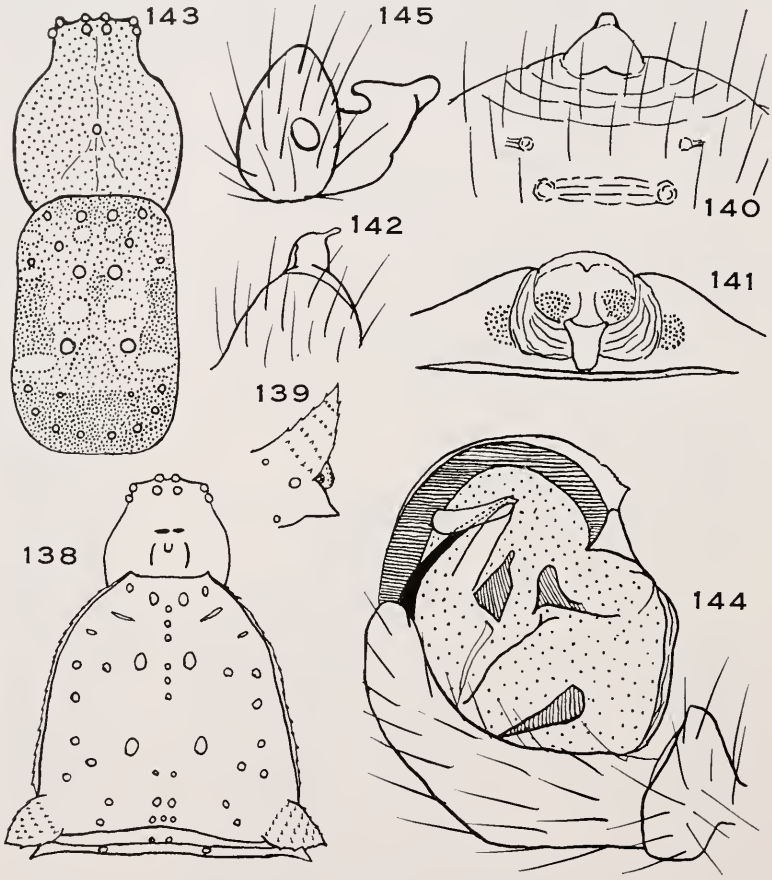
(Figures 138-145)

Acrosoma patruele C. L. Koch, 1839
Plectana patruela Walckenaer, 1841
P. reduviana Walckenaer, 1841
M. reduviana Simon, 1895
M. patruelis F. P.-Cambridge, 1904
M. reduviana F. P.-Cambridge, 1904
A. patruele Banks, 1909
M. patruelis Petrunkevitch, 1911
M. patruelis Reimoser, 1917
M. patruelis Chickering, 1931
M. retracta Chamberlin and Ivie, 1936. New synonymy
M. patruelis Roewer, 1942
M. patruelis Bonnet, 1957

It is quite apparent that much confusion concerning this species has existed in the past and I fear it is not yet entirely removed. I am quite certain that *M. retracta* Chamberlin and Ivie is the same as the species regarded as *M. patruelis* (C. L. Koch), but I am not entirely satisfied that the latter, as now understood, is one species alone. Kraus (1955) has recently identified *M. saccata* (C. L. Koch), 1836 among his collections from El Salvador. It seems to me that this raises the whole question of relationships between these two species and it is my opinion that all available collections of both species should be carefully studied in an endeavor to clarify the whole matter. At present I cannot do better than to consider all specimens which I have had an opportunity to study as belonging to *M. patruelis* (C. L. Koch) as I have indicated.

Female hypotype. Total length 6.305 mm. Carapace only slightly raised behind median thoracic fovea; lateral margins with numerous setigerous tubercles. Sternum moderately convex; lateral tubercles extending toward intervals between second and third coxae, third and fourth, and both fourth coxae quite

marked. Abdomen with a pair of very short anterolateral tubercles where spines so often occur in many species; with a pair of posterolateral spines on each side with the upper one robust and



External Anatomy of *Micrathena*

Figures 138-145, *M. patruelis*

Fig. 138. Dorsal view of body of female.

Fig. 139. Abdominal spines at posterolateral corner.

Figs. 140-142. Epigynum from below, in posterior view, and profile from right side, respectively.

Fig. 143. Dorsal view of body of male.

Fig. 144. Palpal tibia and tarsus of male.

Fig. 145. Palpal tibia and basal tarsal hook in different view.

projecting dorsally and the lower one much smaller and directed posteriorly (Figs. 138-139); lateral margins and more dorsal of the abdominal spines with minute denticles. Epigynum as shown in Figures 140-142. Color in alcohol: Carapace and legs with varying shades of brown; sternum dark brown; abdomen nearly white above because of subchitinous granules but with dark brown or black margins; venter and lateral sides dark brown with many lighter stripes. Considerable variation has been noted among available specimens in respect to color pattern. General appearance shown in Figure 138.

Male hypotype. Total length 3.77 mm. First and second femora with long spines above but only a terminal pair below; with many setigerous tubercles. First and second tibiae with numerous modified spines. Only one prolateral spine on first and second patellae as compared to two on each as mentioned by F. P.-Cambridge. The usual coxal hook and femoral groove and ridge are present. Palpal features are shown in Figures 144-145.

Collection records. The species has been reported from Mexico, through Central America and into northern South America. I have it for study from several parts of Panama, Honduras, Nicaragua, Costa Rica, and Mexico. The male and female hypotypes are both from Barro Colorado Island, C. Z., August, 1936 and July, 1954, respectively.

Micrathena petersi (Taczanowski), 1872

Acrosoma petersi Taczanowski, 1872
A. petersi Keyserling, 1898
M. petersi F. P.-Cambridge, 1904
M. petersi Petrunkevitch, 1911
M. petersi Reimoser, 1917
M. petersi Banks, 1929
M. petersi Roewer, 1942
M. petersi Bonnet, 1957

Taczanowski described this species from Guiana. Keyserling recorded it from Guatemala and described it from an immature female. I have many immature specimens of *M. sexspinosa* (Hahn) which closely resemble Keyserling's figures and description. The specimens identified by Banks (1929) are all immature and, according to my present view, all belong to *M. sexspinosa* (Hahn). For these reasons I am not regarding *M. petersi* (Taczanowski) as a Central American species.

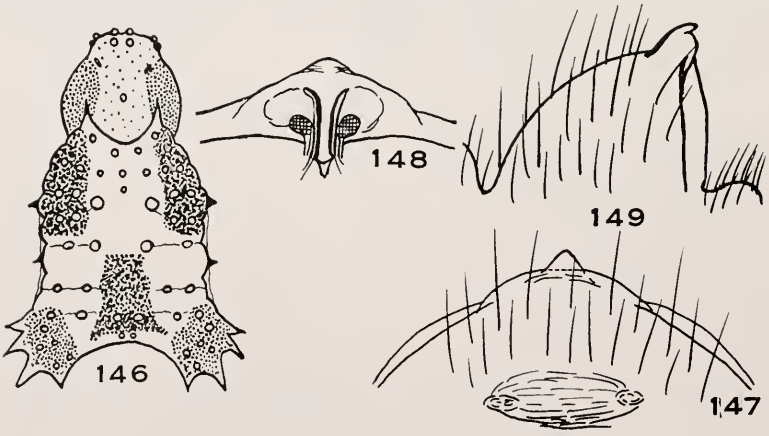
Micrathena quadriserrata F. P.-Cambridge, 1904

(Figures 146-149)

M. quadriserrata Petrunkevitch, 1911
M. quadriserrata Reimoser, 1917
M. quadriserrata Banks, 1929
M. quadriserrata Roewer, 1942
M. quadriserrata Bonnet, 1957

F. P.-Cambridge (1904) had the original specimens from Guatemala; Banks (1929) recorded it from Panama; I have collected it in Panama on several occasions. It has been reported from South America but there seems to be some uncertainty about the exactness of the identifications from this part of the world. The male remains unknown as an adult.

Female hypotype. Total length 6.37 mm. The carapace is very gibbous behind the median fovea. The sternum is slightly convex. Abdomen: there is a pair of long anterior spines extending far over the carapace; two pairs of small lateral marginal spines; the abdomen is bifurcated posteriorly and each bifurcation is subdivided into four fairly robust spines (Fig. 146). The most important epigynal features are shown in Figures 147-149. The



External Anatomy of *Micrathena*

Figures 146-149, *M. quadriserrata*

Fig. 146. Dorsal view of body of female.

Figs. 147-149. Epigynum from below, in posterior view, and in profile from right side, respectively.

most common color pattern is suggested in Figure 146; the unstippled areas are white and the stippled areas are black or gray; numerous specimens show that the color pattern is highly variable; in some the whole dorsum is black. In a specimen in the British Museum (Natural History), collected in Joinville, Brazil, there were a total of nine pairs of spines because of the multiplication of small lateral spines to four on each side. The number and placement of spines in Panamian specimens seem to be quite consistent.

I have several immature males in my collection which I am, for the present, regarding as the missing males in this species but none is sufficiently mature to warrant description.

Collection records. The species has been recorded from both Guatemala and Panama in Central America and from Brazil and Venezuela in South America. I have taken the species repeatedly on Barro Colorado Island, C. Z., at France Field, and at Fort Sheridan, C. Z.

Micrathena saccata (C. L. Koch), 1836

Acrosoma saccatum C. L. Koch, 1836
Plectana saccata Walckenaer, 1841
M. saccata Simon, 1895
M. saccata Petrunkevitch, 1911
M. saccata Reimoser, 1917
M. saccata Roewer, 1942
M. saccata Kraus, 1955
M. saccata Bonnet, 1957

Until recently this species has been considered exclusively South American in distribution. Kraus (1955) reported it from several localities in El Salvador. Of course, caution is indicated here but it seems probable that the species has been confused with *M. patruelis* (C. L. Koch) which it very closely resembles and which is probably very common in El Salvador. For these reasons I am not regarding the species as definitely established in Central America.

Micrathena sagittata (Walckenaer), 1841

(Figures 150-156)

Plectana sagittata Walckenaer, 1841
Epeira spinea Hentz, 1850
Acrosoma bovinum Thorell, 1859
A. bovinum Thorell, 1868

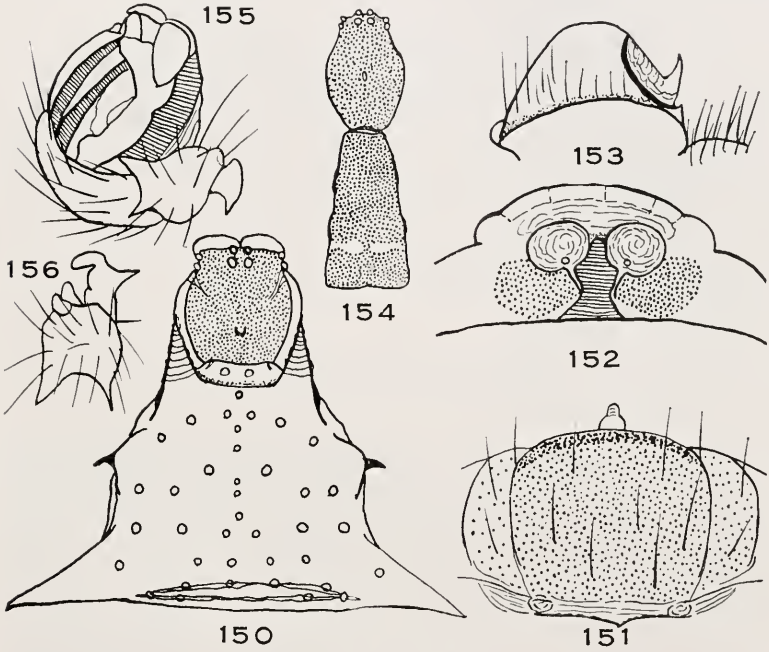
A. spineum Emerton, 1884
A. spineum McCook, 1893
A. spineum Emerton, 1902
M. sagittata F. P.-Cambridge, 1904
M. sagittata Petrunkevitch, 1911
M. sagittata Reimoser, 1917
M. sagittata Petrunkevitch, 1930
M. sagittata Roewer, 1942
M. sagittata Kaston, 1948
M. sagittata Levi, 1954
M. sagittata Bonnet, 1957

This species has been figured and at least partially described many times but the male is not easily separated from that of several other species. *M. sagittata* is widely distributed throughout the United States, Central America, West Indies, and the northern parts of South America.

Female hypotype. Total length 8.45 mm. The cephalic portion of the carapace is prominently raised; considerably gibbous behind the median fovea. The sternum is quite convex; with three pairs of lateral tubercles; the posterior end is strongly tubercular between the bases of the fourth coxae. Abdomen: with a pair of long anterior spines arising from dorsolateral positions (not anterior border) and extending far forward but not closely contiguous to the carapace; a pair of short lateral, somewhat recurved spines arise a little behind the middle; a pair of long robust posterolateral spines; each of the latter has a small cusp at its base (often lacking in certain specimens) (Fig. 150). The epigynum is more distinctive than usual; the free part of the scape appears very different than in most species when viewed in profile (Figs. 151-153). Color in alcohol: dorsum of abdomen largely yellowish with the long spines reddish at bases and black at tips; lateral sides of abdomen with broken stripes of yellow and black; the cephalothorax is reddish brown with a conspicuous whitish yellow margin.

Male hypotype. Total length 4.5 mm. The shape of the body seems to vary somewhat among numerous specimens but the shape of the hypotype is shown in Figure 154 and is regarded as fairly typical. The color is dark brown dorsally with obscure whitish spots as indicated by the unstippled areas. Palp: the tibia is provided with two robust spines, a feature not usually shown in descriptions or published figures; the tarsal hook is rather distinctive (Figs. 155-156). There is no ventral coxal hook on the first coxa and no proximal prolateral groove or

ridge on the second femur (eight males from North Carolina and Colombia examined). Some specimens show the abdominal spines, so conspicuous in females, as plainly suppressed spines in the form of tubercles thus changing the form of the abdomen considerably. This was especially true of the South American forms.



External Anatomy of *Micrathena*

Figures 150-156, *M. sagittata*

Fig. 150. Dorsal view of body of female.

Figs. 151-153. Epigynum from below, in posterior view, and in profile from right side, respectively.

Fig. 154. Dorsal view of body of male.

Fig. 155. Left palpal tibia and tarsus.

Fig. 156. Left palpal tibia and basal tarsal hook in different view.

Collection records. F. P.-Cambridge had the species from Mexico and Guatemala. Specimens from Mexico and Costa Rica are in the collection in the Museum of Comparative Zoology at Harvard College. Petrunkevitch (1930) has recorded it from

Puerto Rico. I found numerous specimens from northern South America in the British Museum (Natural History). It is well known from many parts of the United States. It has not, however, appeared in my Panamanian collections. The male hypotype is from Balsam Gap, North Carolina, August, 1930; the female hypotype is from Vera Cruz, Medias Aquas, Mexico, with no date of collection given.

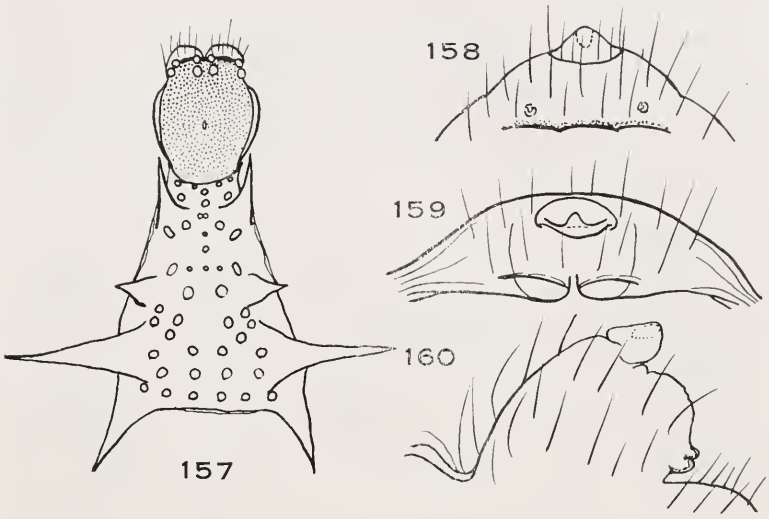
Micrathena schreibersi (Perty), 1833

(Figures 157-168)

Acrosoma schreibersi Perty, 1833
A. spinosum C. L. Koch, 1836
Plectana macracantha Walckenaer, 1841
M. schreibersi Simon, 1895
M. schreibersi F. P.-Cambridge, 1904
M. schreibersi Petrunkevitch, 1911
M. schreibersi Reimoser, 1917
M. schreibersi Banks, 1929
M. coleophora Chamberlin and Ivie, 1936. New synonymy.
M. schreibersi Roewer, 1942
M. schreibersi Bonnet, 1957

This is a well known and strikingly beautiful species characteristic of South America but now known to be one of the most common members of the genus in Panama. Banks, apparently, had the male properly identified but he did not report it in his paper (1929). *M. coleophora* Chamberlin and Ivie is, quite plainly, the male of this species.

Female hypotype. Total length, including the posterior abdominal spines and the somewhat protruding bases of the chelicerae, 14.3 mm. The size appears to be quite variable as determined from a study of a large number of individuals. There are ten spines on the abdomen (Fig. 157). The head portion is strongly raised and the carapace is moderately swollen behind the median fovea. The sternum is only moderately convex with the anterior border swollen into a low transverse ridge. The epigynum is quite distinctive (Figs. 158-160). The color in alcohol is fairly typical of the species in general; the legs are a rich dark brown; the carapace is a similar brown with a yellowish-white margin; the abdomen is yellowish-white in the middle of the dorsum with nearly black margins; the anterior spines are white with the second pair nearly black; the fourth pair is bright red with black tips; the posterior pair is nearly black. The color pattern,



External Anatomy of *Micrathena*

Figures 157-160, *M. schreibersi*

Fig. 157. Dorsal view of body of female.

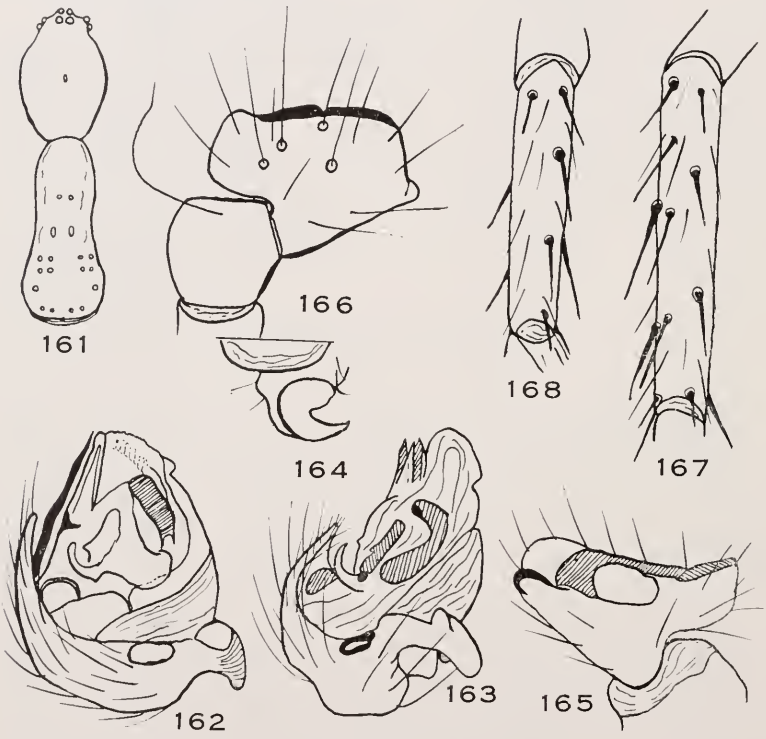
Figs. 158-160. Epigynum from below, in posterior view, and in profile (right side and somewhat more enlarged), respectively.

however, is highly variable as noted in a large series. One specimen from Colombia, for example, had bright yellow legs and a very dark body.

Male hypotype. Total length 5.395 mm. The shape and general appearance (Fig. 161) should serve to identify the males of this species without much difficulty. The color is reddish brown with variations. The abdomen is rounded behind and constricted near the middle. Ventral spines on the first and second tibiae are shown in Figures 167-168. Palp: the tibia appears to be rather distinctive in shape; the basal tarsal hook and other important features of the palpal tarsus are shown in Figures 162-166. There is no ventral hook on the first coxa and no corresponding groove and ridge on the second femur.

Collection records. The species has been reported from numerous localities in South America, Mexico, and Panama. It is probably widely distributed through Central America. It appears to be one of the two most common species of the genus on

Barro Colorado Island, C. Z., but is much less common elsewhere in Panama where I have collected. Both sexes are in my collection from Barro Colorado Island taken from June to August, 1934, 1936, 1939, 1950, 1954 and also in January 1958. I also have it from C. Z. Forest Reserve, 1939; France Field, C. Z., August, 1939; Peluca Hydrographic Station, Boqueron River, Panama, July, 1950.



External Anatomy of *Micrathena*

Figures 161-168, *M. schreibersi*

Fig. 161. Dorsal view of body of male.

Figs. 162-163. Left palpal tarsus and basal tarsal hook; two different views.

Fig. 164. Basal palpal tarsal hook; seen from distal end of tarsus.

Figs. 165-166. Two different views of left palpal patella and tibia.

Figs. 167-168. Right first and second tibiae, respectively, showing spines; seen in ventral view.

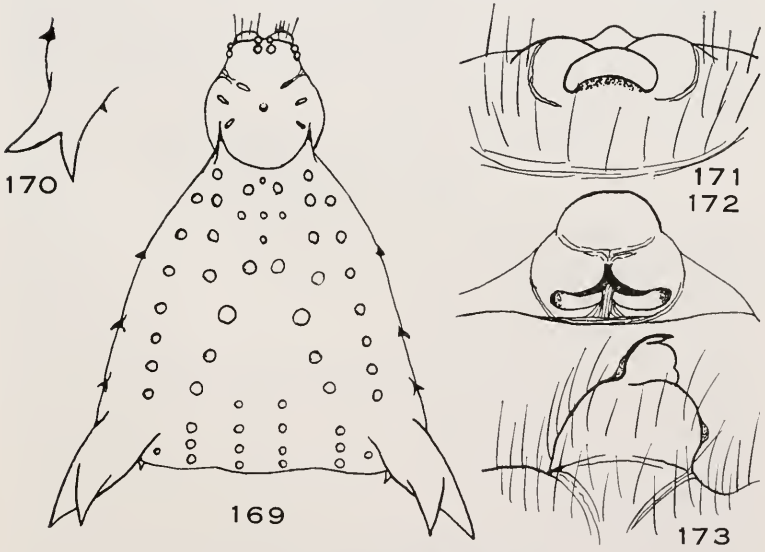
Micrathena serrata F. P.-Cambridge, 1904

(Figures 169-173)

M. serrata Petrunkevitch, 1911
M. serrata Reimoser, 1917
M. serrata Chickering, 1936
M. serrata Roewer, 1942
M. serrata Bonnet, 1957

This species seems to be very uncommon in collections. I had my first opportunity to study the species carefully during my period of work in the British Museum (Natural History) in the summer of 1958. The species was reported from Barro Colorado Island in my collection of 1934 (1936) but the specimens are not now in the collection and, hence, the correctness of the identification cannot now be determined.

Female hypotype. The following facts are taken from a cotype in the British Museum (Natural History): Total length from



External Anatomy of *Micrathena*

Figures 169-173, *M. serrata*

Fig. 169. Dorsal view of body of female.

Fig. 170. Spines at posterolateral corner of abdomen; right side.

Figs. 171-173. Epigynum from below, and in posterior view, and in profile from right side, respectively.

chelicerae to posterior end of abdomen (exclusive of posterior spines) 7.47 mm.; length to tip of posterior spines 8.07 mm. Carapace 2.28 mm. long, 2.08 mm. wide at level of interval between second and third coxae where it is widest. Height of clypeus slightly less than diameter of AME. Carapace considerably raised behind conspicuously rounded central fovea; with three pairs of dorsolateral foveae (Fig. 169). Viewed from in front, anterior row of eyes slightly recurved, posterior row slightly procurved. Chelicerae with four teeth along promargin of fang groove and three along retromargin. Sternum only slightly convex; with posterior end slightly tubercular. Abdomen: extends forward over the carapace a moderate extent; general form and seven pairs of spines as shown in Figures 169-170. Features of the epigynum shown in Figures 171-173. The species would seem to be closely related to *M. duodecimspinosa* (O. P.-Cambridge). The male is unknown.

Collection records. The original specimens were all from the highlands of Chiriqui, El Volcan, Panama. I have recently found two specimens in the Banks collection in the Museum of Comparative Zoology from La Verbena, Costa Rica, (Tristan) which appear to belong to this species.

Micrathena sexspinosa (Hahn), 1822

(Figures 174-180)

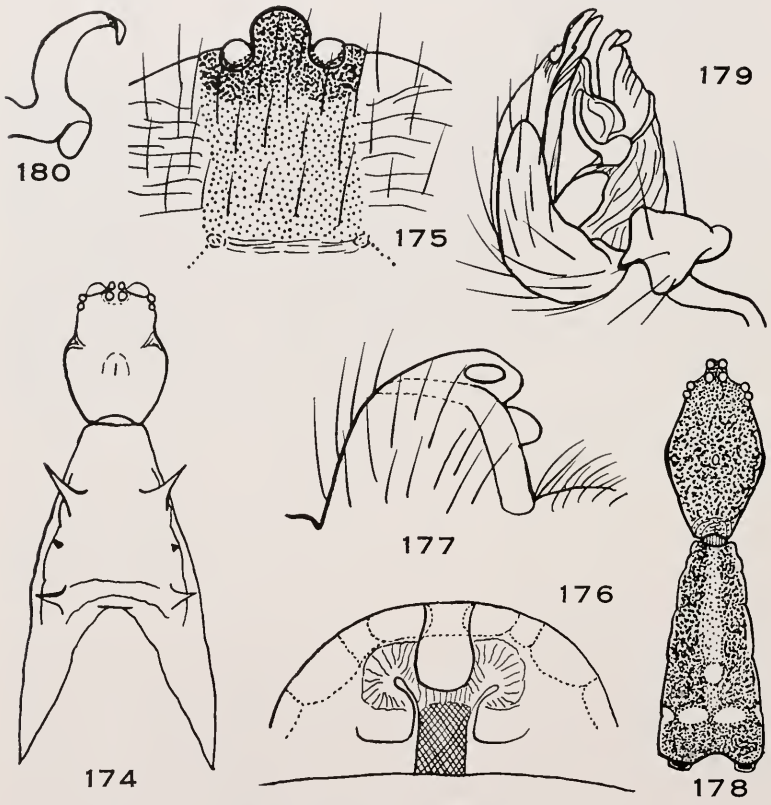
Epeira sexspinosa Hahn, 1822
E. furcata Hahn, 1822
Acrosoma sexspinosa Hahn, 1834
Plectana squamosa Walckenaer, 1841
A. obtusospinosa Keyserling, 1863
Keyserlingia cornigera O. P.-Cambridge, 1890. New synonymy.
A. calcaratum O. P.-Cambridge, 1890
A. obtusospinum Keyserling, 1892
A. calcaratum Keyserling, 1892
A. sedes Getaz, 1893
M. sexspinosa Simon, 1895
M. obtusospina F. P.-Cambridge, 1904
M. cornigera F. P.-Cambridge, 1904. New synonymy.
M. sedes F. P.-Cambridge, 1904
A. obtusispina Banks, 1909
A. sexspinosa Banks, 1909
M. obtusospinosa Petrunkevitch, 1911
M. sexspinosa Petrunkevitch, 1911
M. sedes Petrunkevitch, 1911

M. cornigera Petrunkevitch, 1911. New synonymy.
M. cornigera Reimoser, 1917. New synonymy.
M. sexspinosa Reimoser, 1917
M. cornigera Petrunkevitch, 1925. New synonymy.
M. obtusispina Banks, 1929
M. cornigera Banks, 1929. New synonymy.
M. sexspinosa Petrunkevitch, 1930
M. cornigera Roewer, 1942
M. sexspinosa Roewer, 1942
M. sexspinosa Kraus, 1955
M. cornigera Bonnet, 1957. New synonymy.

It now seems necessary to accept the complicated synonymy the essentials of which are given above but I cannot regard *M. forcipata* (Thorell) as a synonym for *M. sexspinosa* (Hahn) as Reimoser (1917), Roewer (1942), and Bonnet (1957) have done. The Cuban specimens of *M. forcipata* (Thorell) are clearly distinct from *M. sexspinosa* (Hahn), as I shall try to show in a forthcoming paper. The specimens labelled *M. sedes* (Getaz) in the Museum of Comparative Zoology are, in my opinion, all immature females of *M. sexspinosa* (Hahn). Immature females have four pairs of abdominal spines and then, with the last moult the pair between the surviving two pairs of dorsolateral spines is often suppressed. Usually remains of these suppressed spines can be found even in fully matured specimens. Banks (1929) concluded that his *A. cornigera* O. P.-Cambridge was the male of *M. sexspinosa* but he did not formally synonymize it with the latter. Other bibliographers have continued to keep the two separate. Now I think we can be certain of the synonymy as I have given it above.

Female hypotype. Total length 16.25 mm. The cephalic part of the carapace is strongly raised; the median fovea is a shallow groove rather than a pit. The sternum is quite convex; it bears paired tubercles opposite coxae one to three and a posterior tubercle extends between fourth coxae. The femora, especially the first two, are well supplied with setigerous tubercles. The features of the epigynum are shown in Figures 175-177. Abdomen: with three pairs of well developed spines and with another pair represented by tubercles as shown in Figure 174. Color: The carapace is a rich dark reddish brown with a whitish margin; dorsally the abdomen is a mosaic of whitish spots and streaks intermixed with reddish and black spots and streaks; the intermixture is quite variable but rather characteristic of the species.

Male hypotype. Total length 5.59 mm. General form as shown in Figure 178. Color: the dorsal surface is a mahogany brown with light spots and light margin as indicated in the figure. The most distinctive feature appears to be the long curved process belonging to the tarsal hook; this and other palpal features are shown in Figures 179-180. The coxal hook and the corresponding femoral ridge and groove are all lacking.



External Anatomy of *Micrathena*

Figures 174-180, *M. sexspinosa*

Fig. 174. Body of female; dorsal view.

Figs. 175-177. Epigynum from below, in posterior view, and in profile from right side, respectively.

Fig. 178. Body of male; dorsal view.

Fig. 179. Palpal tibia and tarsus of male.

Fig. 180. Basal tarsal hook.

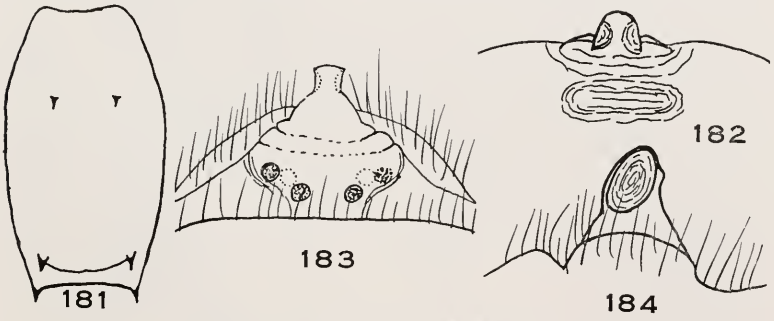
Collection records. The male and female hypotypes are from Barro Colorado Island, C. Z., July and August, 1954, respectively. The species is well known from many localities in Central America, South America, and the West Indies. It appears to be one of the two most abundant species on Barro Colorado Island.

Micrathena spinulata F. P.-Cambridge, 1904

(Figures 181-184)

M. spinulata Petrunkevitch, 1911
M. spinulata Reimoser, 1917
M. spinulata Roewer, 1942
M. spinulata Bonnet, 1957

This species seems to be extremely rare in collections. Apparently it has not been recorded since the original specimens were collected in Mexico and studied by the author of the species. He had only females. During my period of work in the British Museum (Natural History) in the summer of 1958 I found the specimens studied by the author and identified the individual used for F. P.-Cambridge's drawings. This specimen should be regarded as the lectotype and indicated as such.



External Anatomy of *Micrathena*

Figures 181-184, *M. spinulata*

Fig. 181. Abdomen of female; dorsal view.

Figs. 182-184. Epigynum from below, in posterior view, and in profile from right side, respectively.

Lectotype. Total length 6.175 mm. Color pattern essentially as given by the author of the species but I have noted considerable variation in the pattern among the various available specimens. The median thoracic fovea is well defined together with

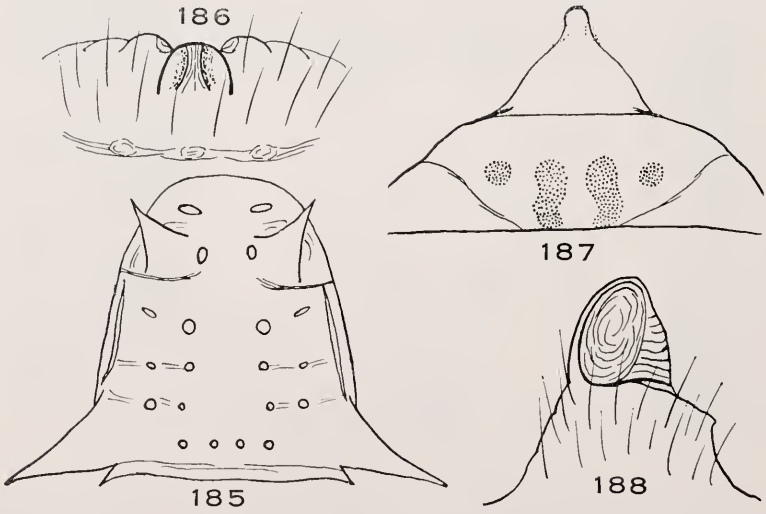
three pairs of dorsolateral foveae. Sternum only slightly convex; only slightly raised opposite the coxae. There are six abdominal spines but all are hardly more than spinules (Fig. 181). The epigynum is similar to that of *M. gracilis* (Figs. 182-184). The species is still only known from Mexico and, as far as I have been able to learn, only from the original collections.

Micrathena striata F. P.-Cambridge, 1904

(Figures 185-188)

M. striata Petrunkevitch, 1911
M. striata Reimoser, 1917
M. striata Roewer, 1942
M. striata Bonnet, 1957

This is another very rare species in collections. My only opportunity to study it also came during my period of work in the British Museum (Natural History) in the summer of 1958. It seems highly probable that I was able to identify the specimen



External Anatomy of *Micrathena*

Figures 185-188, *M. striata*

Fig. 185. Abdomen of female; dorsal view.

Figs. 186-188. Epigynum from below, in posterior view, and in profile from right side, respectively.

which the author of the species used as a basis for his description and I have indicated that this should be designated the lectotype. Numerous specimens from Guatemala are available for study. The total length is about 8 mm. The carapace has a well defined central fovea but no dorsolateral foveae. The sternum is essentially like that of *M. spinulata*. The abdominal spines and general form of the abdomen are shown in Figure 185. The essential features of the epigynum are shown in Figures 186-188. The color of the abdomen is yellow with a series of narrow black lateral lines. The species is apparently known only from Guatemala and only from the female.

Micrathena subflava sp. nov.

(Figures 189-193)

Female holotype. Total length from AME to posterior border of abdomen 8.515 mm. Carapace considerably overlapped by abdomen; about 2.925 mm. long; 2.405 mm. wide opposite interval between second and third coxae where it is widest; strongly gibbous just behind the well defined median fovea; without well defined dorsolateral foveae.

Eyes. Eight in two rows as usual; viewed from above, both rows moderately recurved; viewed from in front, anterior row gently recurved, posterior row gently procurved, all measured by centers. Central ocular quadrangle slightly wider behind than in front, slightly wider behind than long. Ratio of eyes AME : ALE : PME : PLE = 10 : 8.5 : 12 : 8. AME separated from one another by four-fifths of their diameter, from ALE by four times their diameter. PME separated from one another by five-sixths of their diameter, from PLE by ten-thirds of their diameter. Height of clypeus equal to three-fifths of the diameter of AME.

Chelicerae. Robust, quite gibbous in front; typical of females in the genus. With a well defined fang groove having four teeth along the promargin and three along the retromargin (some variation noted between right and left sides).

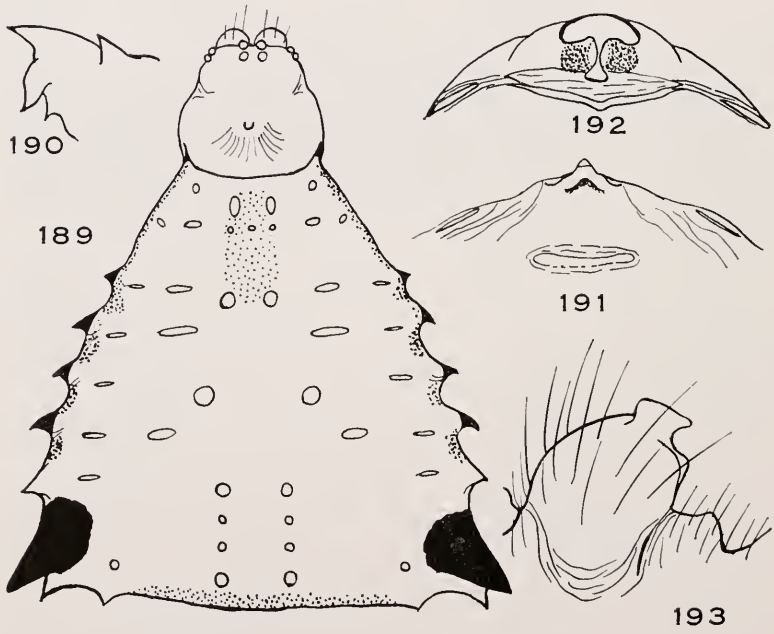
Maxillae and *Lip.* Quite typical of the genus; details regarded as unnoteworthy for adequate description of the species.

Sternum. Moderately convex; with seven tubercles as commonly occur in the genus; continued between fourth coxae which are separated by about three-fourths of their width.

Legs. 4123. Width of first patella at "knee" .29241 mm., tibial index of first leg 10. Width of fourth patella at "knee" .30324 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
1.	2.925	.975	1.950	1.625	.740	8.215
2.	2.470	.942	1.570	1.495	.740	7.217
3.	1.950	.650	.975	.910	.585	5.070
4.	3.250	.845	1.755	1.950	.750	8.550

With many setigerous tubercles on legs but only a few spines with details of spination regarded as unnoteworthy.



External Anatomy of *Micrathena*

Figures 189-193, *M. subflava*

Fig. 189. Body of female; dorsal view.

Fig. 190. Spines at posterolateral angle of abdomen; lateral view.

Figs. 191-193. Epigynum from below, in posterior view, and in profile from right side, respectively.

Abdomen. General features as shown in Figures 189-190. Considerably flattened dorsoventrally; only slightly concave in middle of posterior dorsal region; with nine pairs of short spines as figured but the first pair of lateral marginal spines is often reduced to blunt tubercles in paratypes. A prominent tubercle or short robust spine lies on each side of the chitinous cone surrounding the spinnerets.

Epigynum. The general characteristics of this organ are shown in Figures 191-193.

Color in alcohol. Legs, in general, a dull brown with some variations; sternum a dusky yellow; carapace yellowish with fine brownish dots. Abdomen: main part of dorsum yellowish with variations; irregularly black along the lateral margins and posterior border; lateral sides with narrow broken black stripes alternating with yellowish stripes; region of epigynum and cone around spinnerets reddish brown.

Type locality. Holotype female from Barro Colorado Island, C. Z., August, 1950. Several paratype females from the same locality: June, 1934; June-August, 1936; June, 1939; July-August, 1954. The male is unknown.

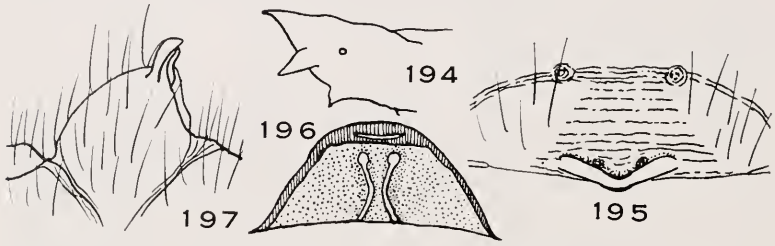
Micrathena subspinosa F. P.-Cambridge, 1904

(Figures 194-197)

M. subspinosa Petrunkevitch, 1911
M. subspinosa Reimoser, 1917
M. subspinosa Roewer, 1942
M. subspinosa Bonnet, 1957

The correct treatment of this species is not at all clear. I have wavered between the decision to regard it as a variant of *M. duodecimspinosa* (O. P.-Cambridge) and retaining it as a valid species and have finally decided on the latter course, at least for the present. I had an opportunity to study the type in the British Museum (Natural History). The author of the species gave the important features very briefly as follows: "almost precisely similar to *M. 12-spinosa* in general character, but the third, lower cusp on the posterior bifid spur is remote from the two main cusps in the middle of the spur behind, and thus becomes trifid. The posterior margin of the vulva, though presenting a minute median angle, has not a tongue-like prominence which is noticeable in *M. 12-spinosa.*" Color: "similar to that of *M. 12-spinosa,* the posterior spurs dark brown, apically black."

The length is about 6 mm. Figure 194 is intended to show relationships among the spines at the posterolateral angle of the abdomen. Figures 195-197 are intended to show the chief features of the epigynum. Known only from Guatemala and only from the female.



External Anatomy of *Micrathena*

Figures 194-197, *M. subspinosa*

Fig. 194. Spines at posterolateral angle of abdomen; lateral view.

Figs. 195-197. Epigynum from below, in posterior view, and in profile from right side, respectively.

Micrathena trapa (Getaz), 1891

Acrosoma trapa Getaz, 1891
M. trapa F. P.-Cambridge, 1904
M. trapa Petrunkevitch, 1911
M. trapa Reimoser, 1917
M. trapa Roewer, 1942
M. trapa Bonnet, 1957

F. P.-Cambridge (1904) did not include any description of this species and did not include it in his keys. The brief description given by Reimoser (1917) was copied from the statement given by the author of the species and gives little basis for its recognition. It seems probable that the species exists among others which are better known and well described. The male is unknown. I have been obliged to omit the species from further consideration in this paper.

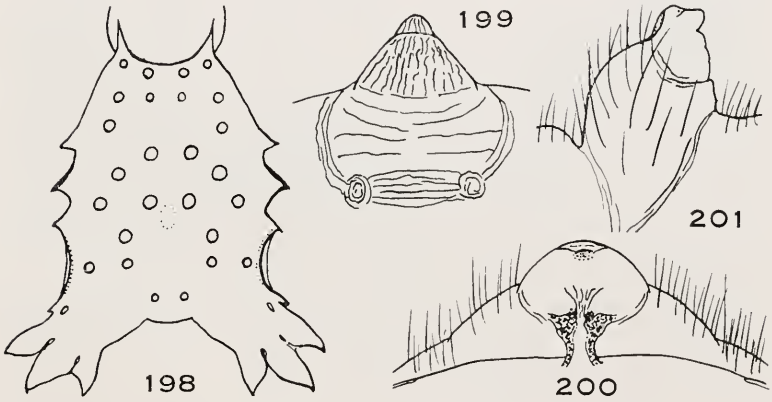
Micrathena triserrata F. P.-Cambridge, 1904

(Figures 198-201)

Acrosoma triserrata Banks, 1909
M. triserrata Petrunkevitch, 1911
M. triserrata Reimoser, 1917

M. triserrata Roewer, 1942
M. triserrata Bonnet, 1957

Specimens in the Pickard-Cambridge collection from Guatemala and Costa Rica have been studied and a lectotype selected. The following facts are taken from the lectotype in the British Museum (Natural History): Total length from AME to posterior end of the triserrated abdominal fork 8.13 mm. Carapace with a well defined central fovea behind which is a marked gibbosity; there are also three pairs of dorsolateral foveae; the head is considerably raised and separated from the thoracic part by diagonal grooves. The sternum is only slightly convex and somewhat granulose. In addition to the abdominal spines shown in F. P.-Cambridge's figures and named in his description is, apparently, a small lateral marginal spine at base of the fork on each side (Fig. 198), but it appears to be somewhat variable.



External Anatomy of *Micrathena*

Figures 198-201, *M. triserrata*

Fig. 198. Abdomen of female; dorsal view.

Figs. 199-201. Epigynum from below, in posterior view, and in profile from right side, respectively.

On the lectotype this small spine is unilateral (possibly lost in handling), barely represented in one paratype, and lacking on the third specimen. Features of the epigynum are shown in Figures 199-201. The male is unknown. The species is known only from Guatemala and Costa Rica.

Micrathena uncata F. P.-Cambridge, 1904

(Figures 202-205)

M. uncata Petrunkevitch, 1911
M. uncata Reimoser, 1917
M. uncata Roewer, 1942
M. uncata Bonnet, 1957

This is another species which appears in collections only very rarely. Apparently it has not been reported until the present time since its first appearance in the collections studied by F. P.-Cambridge (1904). I appear to have two specimens which belong here. Only males are known.

Male hypotype. Total length 4.5 mm. The general appearance (Fig. 202) is similar to that of *M. parallela* (O. P.-Cambridge). The first two pairs of tibiae do not have the modified short ventral spines recorded by F. P.-Cambridge; the first pair of femora has a series of ventral and prolateral spines probably modified for clasping (Fig. 203); the second pair of femora seems to be devoid of these; the ventral hook is lacking on the first coxa and the corresponding ridge and groove on the second femur are also lacking. The main features of the palpal tarsus are shown in Figures 204-205. Color: Carapace with a broad, median, light brownish stripe and a broad brown stripe on each side (Fig. 202); the abdomen is light yellowish dorsally and with numerous irregular white flecks and small indications of black spots at anterior and posterolateral corners.

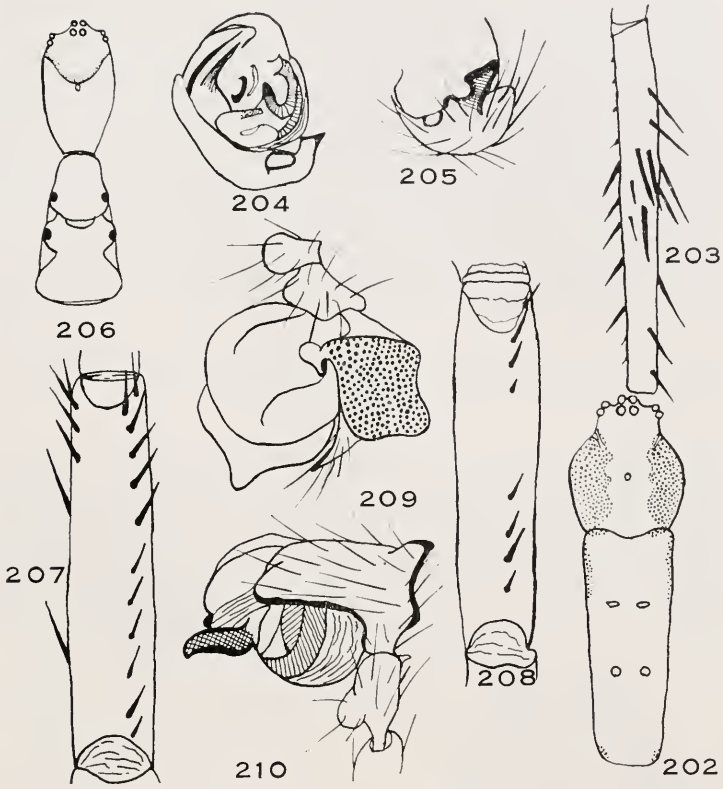
Collection records. F. P.-Cambridge had this species only from Guatemala. The hypotype and one other specimen are from Barro Colorado Island, C. Z., August, 1939.

Micrathena vitiosa (O. P.-Cambridge, 1890)

(Figures 206-210)

Acrosoma vitiosum O. P.-Cambridge, 1890
A. vitiosum Keyserling, 1892
M. vitiosa F. P.-Cambridge, 1904
M. vitiosa Petrunkevitch, 1911
M. vitiosa Reimoser, 1917
M. vitiosa Roewer, 1942
M. vitiosa Bonnet, 1957

While working in the British Museum (Natural History) in the summer of 1958 I had my only opportunity to study this



External Anatomy of *Micrathena*

Figures 202-205, *M. uncata*

Figures 206-210, *M. vitiosa*

Fig. 202. Dorsal view of body of male.
Fig. 203. Left first femur; ventral and prolateral spines.
Fig. 204. Left palpal tarsus.
Fig. 205. Another view of basal tarsal hook.
Fig. 206. Dorsal view of body of male (from O. P.-C.).
Figs. 207-208. First and second femora, respectively; ventral views.
Figs. 209-210. Right palpal patella, tibia, and tarsus; 209 especially to show form of basal tarsal hook.

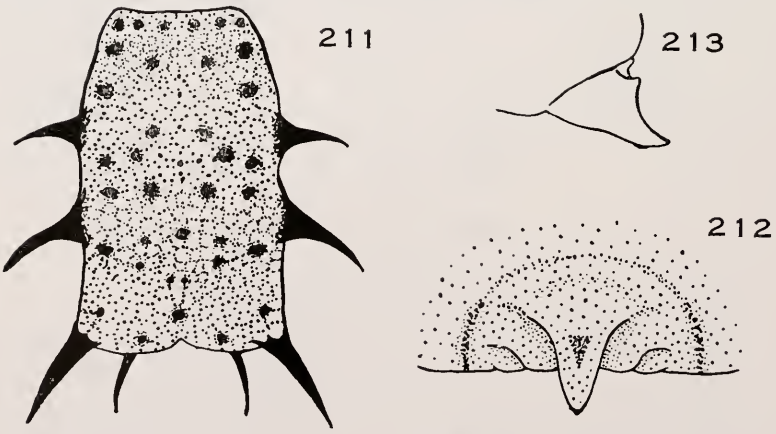
species. I found two specimens in the Cambridge collection and one of these should be selected as the lectotype. The Pickard-Cambridges had the species from Panama and Keyserling

(1892) reported it from Guatemala but I did not find these specimens in the Keyserling collection. The total length is about 4.5 mm. The general form of the body is shown in Figure 206. The first and second tibiae appeared to be spined in what may be termed the usual manner. The first and second femora, however, seemed to have special ventral spines as shown in Figures 207-208. The third femur also has a row of spur-like ventral spines. The most important features of the palp are shown in Figures 209-210. The tarsal hook is particularly distinctive. There is no ventral hook on the first coxa nor any ridge or groove on the second femur. The female is completely unknown.

Micrathena zilchi Kraus, 1955

(Figures 211-213)

The holotype and several mature paratypes as well as several more immature specimens were reported by Dr. Kraus in 1955 from El Salvador. I know of no mature specimens of this species in American collections. I have one immature female from Honduras which I am tentatively assigning to this species. Only females are known. Some of the distinctive features of the species, taken directly from the original description, may be



External Anatomy of *Micrathena*

Figures 211-213, *M. zilchi*

Fig. 211. Dorsal view of abdomen of female.
Figs. 212-213. Epigynum from below and in profile, respectively.

given as follows: Total length 14 mm.; central ocular quadrangle almost square; PME larger than AME; general shape of abdomen and spination as shown in Figure 211; the epigynum appears as shown in Figures 212-213; the color of the abdomen is bright, reddish yellow. The author of the species regards it as closely related to *M. xanthopyga* Simon, 1895 from Venezuela. The accompanying figures have been copied directly from those furnished with the original description.

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AT HARVARD COLLEGE
Vol. 125, No. 14

THE PROSCALOPINAE, A NEW SUBFAMILY OF TALPID INSECTIVORES

By Katherine M. Reed

With Two Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
November, 1961

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No. 14 — *The Proscalopinae, a new Subfamily of Talpid Insectivores*

By Katherine M. Reed

INTRODUCTION

In the course of work on the insectivores of the Split Rock local fauna of Wyoming (Reed, 1960), I had an opportunity to examine the known material of *Proscalops* and its relatives. Matthew (1928, pp. 70-71) suggested in passing that the forms known to him might constitute a new family, although he considered this conjectural. With the discovery of at least three more of these highly distinctive forms since Matthew's time, the evidence now available indicates that at least a new subfamily of the Talpidae must be erected for the group.

I am indebted to the authorities of the American Museum of Natural History, the Chicago Natural History Museum, the Kansas University Museum of Paleontology, and Amherst College for the loan of specimens. Dr. Charles A. Reed, Dr. William Turnbull, Dr. Reid Macdonald, Dr. Paul O. McGrew and Dr. Raymond Alf all kindly assisted me with information about material in their collections. I also wish to thank Prof. Bryan Patterson and Mr. Craig C. Black for their help in this study, and the Mammal Department of the Museum of Comparative Zoology for access to Recent talpid and chrysochlorid material. I am also grateful to Prof. Harry B. Whittington for his assistance with the photography.

The following abbreviations are used:

A.C.M., Amherst College Museum; A.M.N.H., American Museum of Natural History; C.N.H.M., Chicago Natural History Museum; K.U.M.V.P., Kansas University Museum of Vertebrate Paleontology; M.C.Z., Museum of Comparative Zoology; l., length, antero-posterior; w., width, transverse; trig., trigonid; tal., talonid.

TAXONOMY

Family TALPIDAE

PROSCALOPINAE, subfam. nov.

Type genus. Proscalops Matthew, 1901.

Diagnosis. Skull chrysochlorid-like; dentition of talpid type.

Skull wide and deep in posterior part; flexure in maxillary, between P^3 and P^4, stronger than in *Neurotrichus;* lateral projections on premaxillaries; slight sagittal and occipital crests; palate long relative to skull length; antorbital rim confined to maxillary, not joining main body of zygoma. Wide lingual shelf on upper molars with hypocone varyingly developed; dental formula $I\frac{3}{?}$ $C\frac{1}{1}$ $P\frac{3}{?}$ $M\frac{3}{3}$.

Included genera. Proscalops Matthew, 1901; *Mesoscalops* Reed, 1960; *Oligoscalops* gen. nov.

Range. Mid-Oligocene to mid-Miocene, North America.

Only *Proscalops miocaenus* and *Mesoscalops scopelotemos* have hitherto been clearly diagnosed. Diagnoses of all species, in order of their chronologic appearance follow.

Oligoscalops gen. nov.

Type species. Oligoscalops whitmanensis sp. nov.

Range. Mid-Oligocene, Wyoming and Colorado.

Diagnosis. Roots of P^3 partially divided, tooth laterally compressed, abutting against P^4; P^4 with large parastylar area and lingual cusp situated at mid-line; protocones of molars directed antero-internally; M^2 wider than long; metastyle of M^3 subparallel to line joining protocone and metacone; hypocone rudimentary.

Oligoscalops whitmanensis sp. nov.

Type. C.N.H.M. no. P 25800, partial skull and jaws.

Hypodigm. Type and K.U.M.V.P. no. 8143, left ramus with P_2-M_3.

Horizon and locality. Mid-Oligocene, type from Brule fm., Whitman, Niobrara County, Wyoming, collected by Dr. Paul O. McGrew. K.U.M.V.P. no. 8143 from middle Cedar Creek member of White River fm., W 1/2 sec. 7, T 11 N, R 53 W, Logan County, Colorado, collected by Dr. Edwin C. Galbreath.

Diagnosis. As for the genus; the smallest known member of the Proscalopinae.

Measurements (in millimeters).
C.N.H.M. no. P 25800

M^1 left l. 2.2	M^3 left l. 1.4
w. 1.7	w. 1.4
right l. 2.1–	right l. 1.4
w. 1.65	w. —
M^2 left l. 1.7	M_2 right l. 1.95
w. 2.0	w. trig. 1.35
right l. 1.8	w. tal. 1.35
w. 2.1	

Skull width at M^2: 9.0
K.U.M.V.P. no. 8143

Ml left 1.–	M_3 left l. 1.5
w. tal. 1.0	w. trig. 1.3
M_2 left l. 2.1	w. tal. 0.9
w. trig. 1.7	
w. tal. 2.1	

Proscalops Matthew

Type species. Proscalops miocaenus Matthew.

Range. Late Mid-Oligocene to early Miocene.

Emended diagnosis. Lateral premaxillary projections dorsoventrally compressed; diastema between P^3 and P^4; P^3 small, oval, single rooted; P^4 lacking parastylar area with lingual cusp anterior to mid-line; upper molars with or without well developed hypocones; parastyles incipient on M^1, definite on M^2.

Proscalops miocaenus Matthew

Matthew, 1901, pp. 375-376, figs. 1-2; 1909, pl. 49, fig. 5; Galbreath, 1953, p. 49.
2 MCZ (Reed 6007 Mre7 Aug7

Type. A.M.N.H. no. 8949a, broken skull and jaw.

Hypodigm. Type only.

Horizon and locality. Mid-Oligocene, Vista beds, Cedar Creek, Logan County, Colorado, collected by Dr. W. D. Matthew.

Emended diagnosis. Smallest known species of the genus. P^4 relatively narrower than in *Proscalops tertius*, lingual cusp directed posteriorly; lingual portions of upper molars narrower than in other species of the genus, with hypocones and protostyles less developed. M^3 compressed antero-posteriorly, lingual portion narrow, hypocone rudimentary.

Measurements (in millimeters).

A.M.N.H. no. 8949a

P^4 left l. 2.0	M^2 right l. 2.2
w. 1.7	w. 2.7
right l. 2.0	M^3 right l. 1.5
w. 1.8	w. 1.8
M^1 right l. 2.8	
w. 2.5	

Palatal width at M^2: 9.4 (from Matthew, 1901, p. 376).

Proscalops tertius sp. nov.

Type. A.M.N.H. no. 19420, partial skull and left ramus with M_{1-3}.

Hypodigm. Type only.

Horizon and locality. Oligocene, "White River fm.," possibly Brule, "Badlands, South Dakota," collected by Dr. G. L. Jepsen. No more precise information is available.

Diagnosis. Teeth very slightly larger and hypocones better developed than in *Proscalops secundus;* lingual cusp of P^4 essentially conical, larger than in *P. miocaenus*, no part extending anterior to labial cusp; metaconid of M_2 with minute metastylid, wide opening of talonid valley to interior as in *Mogera wogura*.

Measurements (in millimeters).

A.M.N.H. no. 19420

P^4 left l. 2.1	M^3 left l. 2.4
w. 2.1	w. —
right l. 2.1	right l. 2.1
w. 2.2	w. 2.1
M^1 left l. 3.2	M_1 left l. 2.85
w. 2.7	w. trig. 1.6
right l. 3.2	w. tal. 2.05
w. 2.8	M_2 left l. 2.7
M^2 left l. 2.8	w. trig. 1.8
w. 2.65	w. tal. 2.1
right l. 2.9	M_3 left l. 2.2
w. 2.75	w. trig. 1.6
	w. tal. 1.3

Skull width at M^2: 12.0

Proscalops secundus Matthew

Matthew, 1909, p. 559, pl. 51, figs. 3, 4; Galbreath 1953, p. 49.

This species has never been formally described or diagnosed. As Galbreath points out (1953, p. 49, footnote) "the type designation and specific name must be cited as figures 3 and 4 of plate 51, and the accompanying legends on page 559 of 'The Carnivora and Insectivora of the Bridger Basin Middle Eocene' (Matthew, W. D., 1909, Am. Mus. Nat. Hist. Mem., vol. 9, pt. 6)."

Type. A.M.N.H. no. 13798.

Hypodigm. Type only.

Horizon and locality. Early Miocene, "lower Rosebud" of Matthew, Bear-in-the-lodge Creek, South Dakota, collected by Dr. W. D. Matthew.[1]

Emended diagnosis. Larger than *P. miocaenus;* lingual cusp of P^4 broader and extending farther anteriorly than in *P. miocaenus*, about as in *Mesoscalops scopelotemos;* lingual portion of M^{1-3} broader, and hypocones better developed on M^{1-2} than in *P. miocaenus;* posterior root of zygomatic arch joining flange extending up side of cranium.

Measurements (in millimeters).

A.M.N.H. no. 13798

P^4 left l. 1.85	M^1 left l. 3.1
w. l. 1.6	w. 2.6
right l. 1.9	right l. 2.7
w. 1.6	w. 2.5
M^2 left l. 2.55	M^3 left l. 2.3
w. 2.8	w. 1.9
right l. 2.4	right l. 2.2
w. 2.8	w. 1.8

Skull width at M^2: 10.7; skull is slightly crushed transversely.

Mesoscalops Reed

Type species. Mesoscalops scopelotemos Reed 1960.

Range. Mid-Miocene, Wyoming.

Diagnosis. In general similar to *Proscalops*, but differing as follows: protocone of upper molars more rounded and somewhat larger than hypocone, situated more nearly directly internal to

[1] Macdonald (pers. comm.) suggests that the horizon may be either Monroe Creek formation or Harrison formation.

paracone, imparting a square appearance to the outline of teeth; P^4 with lingual face faintly grooved and with wide lingual shelf; lower molars with small median cingulum just above gum line between hypo- and protoconids, talonid of M_1 wider than trigonid.

Mescoscalops scopelotemos Reed

Reed, 1960, pp. 2-4, 7-8, pl. 1, pl. 2, figs. 1, 2.

Type. A.C.M. no. 10461, isolated left M^1.

Hypodigm. Type and numerous isolated teeth including P^4-M^3, $M_{1\text{-}3}$. (See Reed 1960, p. 2).

Horizon and locality. Mid-Miocene; NW 1/4 sec. 36, T 29 N, R 90 W, Fremont County, Wyoming, from the vicinity of the *Brachycrus* quarry seven miles west of Muddy Gap filling station, in a draw about 1/4 mile south of U.S. highway 287.

Diagnosis. As for the genus.

Measurements. See Reed 1960, pp. 7-8.

MORPHOLOGY

The subfamily Proscalopinae is at present represented only by skulls and partial rami or by isolated teeth. Leaving aside for the moment the possible but questionable association of *Arctorycles-Cryptorycles* with these forms, there are no postcranial elements known to me that can definitely be assigned to the species.

The skull

No sutures can be detected in any of the specimens, a situation not uncommon among small fossorial forms. The anterior portion of the skull is preserved only in *Proscalops secundus* and *Oligoscalops whitmanensis*. The two are similar in having lateral projections on the premaxillaries. In *Oligoscalops* these projections are abraded and now extend to a point above the roots of I^1; it is unlikely that they extended farther forward. The lateral projections are only faintly demarcated from the dorsal surface of the snout; a slight groove partially separates the nasals and the projections posteriorly. The lateral projections in *P. secundus* are more distinct than in the earlier form. As preserved, they extend slightly beyond I^1. The processes form conspicuous projecting shelves, flat dorsally, situated well below the level of the nasals. The edges of the projections tip

upward very slightly. These projections are distinctly different from any structures in the same area in other talpids. There are slight dorsal swellings in the premaxillaries of the various talpids examined — *Scapanus*, *Parascalops*, *Talpa*, *Neurotrichus*, *Condylura*, *Scalopus*, *Mogera*, *Uropsilus*, *Desmana*, *Galemys*, *Rhynconax* — but in no case would these swellings significantly change the round or squarish outline of a transverse section through the anterior part of the skull. A similar section through either of the fossil skulls would give an elliptical section with the major axis horizontal. The projections are more nearly comparable to the premaxillary projections of the chrysochlorids, but here too there are distinct differences. The narial opening of the Proscalopinae is situated immediately above the incisors with no antero-dorsally inclined bony shelf above I^1, such as occurs in the African chrysochlorids, especially in *Chlorotalpa*. In *Amblysomus* and *Eremitalpa* the lateral projections are on the same level as the nasals and tend to converge ventro-medially, rather than more medially as in the Proscalopinae. In all chrysochlorids the projections extend beyond the tooth-bearing portion of the premaxillary, and in none are the projections as distinctly differentiated from the general outline of the skull as they are in *P. secundus*. *Oligoscalops* more nearly resembles the chrysochlorids in this latter respect. In a specimen of *Eremitalpa* (M. C. Z. no. 39614), the cartilage of the rhinarium remains. The cartilage is attached to the premaxillaries ventrally and the nasals dorsally; it is supported ventro-laterally by the lateral projections. It is likely that the projections in the Proscalopinae served a similar purpose. The similarity in structure to the chrysochlorids thus suggests a nasal region more chrysochlorid-like than mole-like.

On the skull of *Oligoscalops* there are two slight depressions above I^3, one on either side. These are on the dorsal side of the premaxillary and are slightly deeper antero-medially than posteriorly. Analogous depressions are not immediately evident on *P. secundus*, but may be represented by the dorsal surface of the lateral projections and possibly the vertical portions of the premaxillary medial to the projections. Nothing similar occurs either in talpids or in chrysochlorids.

When the skulls of *Proscalops secundus*, *Oligoscalops whitmanensis*, and *Proscalops tertius* are viewed in profile, a feature common to all can be seen, namely, a notable difference in the

depth anteriorly and posteriorly. This difference can be measured only in *P. secundus* and *tertius*, where the cranial region is reasonably complete, but a similar difference is clearly suggested in *Oligoscalops*. The difference between the two dimensions is above or at the upper limit of similar measurements in both talpids and chrysochlorids.

The tooth row in the Proscalopinae shows a flexure or arching between P^3 and P^4, even more pronounced than in *Neurotrichus*. Anterior to P^4, the tooth row tends to parallel the dorsal profile of the antorbital portion of the skull. Posterior to P^4 the tooth row and the skull profile diverge, the tooth row descending. This characteristic can be seen in all the skulls, even in that of the poorly preserved *P. miocaenus;* it is best shown by *P. secundus*. This flexure occurs at the shallowest part of the skull. A similar flexure cannot be found in other talpids except *Neurotrichus*, or in the chrysochlorids.

The structure of the zygomatic arch distinguishes the Proscalopinae both from other talpids and from the chrysochlorids. The anterior part of the zygoma is preserved in all the available skulls. The anterior part of the arch in all is slender and rounded, stouter than in Recent talpids, but not as deep as in the chrysochlorids. The entire arch is preserved on the left side of *P. miocaenus;* it maintains its diameter throughout as in modern talpids, the cross-section of the posterior root being essentially the same as that of the anterior. In *P. tertius*, the left side of the skull preserves a small rounded posterior root; the right side corresponds, although badly worn. *P. secundus* likewise preserves a small rounded posterior root. This is a notable difference from chrysochlorids in which the arch increases greatly in depth posteriorly. The arch in the fossil forms shows no upward bending as in *Uropsilus* or *Rhynconax*. The facial regions of *P. secundus*, *P. tertius* and *Oligoscalops* are widest at the level of M^2. The zygomatic arch leaves the side of the facial region above the posterior margin of M^2, as in *Scapanus californicus* and *Uropsilus*. In all other talpids, the arch leaves opposite M^3 or the posterior margin of the tooth row. In chrysochlorids the arch begins above M^2, except in *Eremitalpa*. The antorbital border, which, due to the size of the infra-orbital foramen, forms a bar as in other insectivores, does not reach to the zygoma but joins the main body of the maxillary medial to the zygoma. The bar has a very slight posterior slant to it. This feature of the skull is in decided contrast to the Talpinae, Condylurinae and Scalopinae and to the chrysochlorids in which not only does the bar join the zygoma,

but it also has a distinct posterior slant, uniting with the arch posterior to the tooth row. In *Mogera*, the bar appears to be attached to the side of the facial region, but here the posterior slant is greater than in the Proscalopinae. In *Uropsilus*, however, the bar is stout, posterior to the infraorbital and the large lacrymal foramina and joins the maxillary. It does not make up any part of the zygoma. The bar in *Desmana* joins medial to the rim of the zygoma, but is not attached to the maxillary.

In *P. secundus*, there is evidence of a squamosal flange extending up the side of the skull, suggestive of the chrysochlorid condition. However, the zygoma plays no part in the formation of the flange in *P. secundus* as it does in the chrysochlorids. It is impossible to determine the original width due to breakage. Matthew's figure (1909) shows that some of this flange has been lost since the photograph was made. The dorsal part of the flange is lacking, but it is probable that it extended to the slight sagittal crest present in this form. At a point approximately one-third of the distance between the glenoid fossa and the sagittal crest there is a buttress that divides the depression made by the flange into two portions, the ventral evidently deeper than the dorsal. A somewhat similar buttress is found in *Amblysomus* and *Eremitalpa* at the point where the flange joins the side wall of the cranium. However, the flange in *P. secundus* undoubtedly did not end at the buttress but continued toward the sagittal crest becoming progressively shallower dorsally. It is probable that the squamosal in this form resembled that of the large chrysochlorid, *Chrysospalax*, rather than the smaller forms, in the degree of projection from the skull, as shown in Matthew's figure. *Desmana*, which has both a sagittal crest and lateral, nearly horizontal flanges at the extremities of the occipital crest, does not in the least resemble *P. secundus* in this region.

The occipital region of the *Proscalopinae*, best seen in *P. secundus*, shows some resemblance to both talpids and chrysochlorids. The fossil skull preserves a trace of the occipital crest found in Recent talpids, especially prominent in *Desmana*. This crest is not found in the chrysochlorids; instead there is a crest which follows, essentially, the fronto-parietal suture above and the junction of the squamosal and the posterior part of the zygoma below. This crest is also present in the Proscalopinae.

The palate in the Proscalopinae extends posteriorly to a line joining the posterior borders of M^3, as in *Neurotrichus*. This character easily distinguishes the Proscalopinae from *Talpa*,

Mogera, *Uropsilus*, *Desmana* and *Scalopus*, in which the palate ends well posterior to M^3, or from *Condylura* in which the palate ends anterior to M^3. The chrysochlorids resemble *Talpa*, etc., in this respect. The incisive foramen in *P. secundus* and *Oligoscalops* is situated immediately medial to a point between I^{1-2}. The incisive foramen is more posterior in chrysochlorids. The posterior palatal foramina can be seen in *P. secundus* and *Oligoscalops;* they occur on a line joining the postero-labial roots of the first molars. There are no palatal vacuities. Although neither the skull of *P. secundus* nor that of *Oligoscalops* is complete or free from distortion, it is obvious on inspection that the palate is longer relative to the total skull length and to basicranial length than in Recent talpids or in chrysochlorids (Table I).

TABLE I

Genus	Length of palate in cm.	Length of basicranium in cm.	Basicranium/Palate
Proscalops secundus	1.54	1.23	.79
Oligoscalops whitmanensis	1.14	1.0	.88
Scapanus	1.53	2.1	1.3
Scalopus	1.43	1.69	1.17
Condylura	1.32	1.95	1.4
Mogera	1.59	2.44	1.4
Neurotrichus	1.0	1.23	1.2
Parascalops	1.38	1.79	1.3
Talpa	1.33	1.96	1.4
Uropsilus	1.0	1.14	1.14
Desmana	3.20	2.56	1.25
Chrysospalax	1.74	1.67	.96–
Amblysomus	1.22	1.23	1.00
Eremitalpa	0.87	1.0	1.1
Chlorotalpa	0.86	1.23	1.4

The condylar region of most Recent talpids easily distinguishes them from the Proscalopinae. With the exception of *Mogera*, the condyle is neither as stout nor as ventrally inclined a structure as in the fossil forms. Recent talpids also possess a small depression at the anterior end of the condyle, a feature not seen in the Proscalopinae. Chrysochlorids resemble the Proscalopinae

in the structures of this region. The foramen magnum in Recent talpids has a notable nick that extends anteriorly to the level of the posterior lacerate foramen or even slightly anterior to it. The corresponding nick in the Proscalopinae extends to a similar position but is much less pronounced, due to the more ventral position of the condyle. The same is true of the chrysochlorids. The condylar and posterior lacerate foramina in the Proscalopinae are situated close to the condyle; the former is a narrow slit just above the articular area of the condyle. The position of these foramina is similar to that in Recent talpids. The carotid foramen is closer and more nearly lateral to the condylar and posterior lacerate foramina in the fossils than in *Scalopus* and other Recent talpids, but is not greatly different in position from that of the chrysochlorids. The carotid artery seems to enter the posterior wall of the bulla as in the talpids. It is the most conspicuous foramen in the skull.

The bullae of *P. tertius* are irregularly quadrangular in outline and are neither as inflated as in the chrysochlorids nor as flattened as in Recent talpids. They bear rounded crests that run medially from the external auditory meatus, the anterior and posterior parts of the bullae sloping upwards from the crests. In *Oligoscalops* the bullae are less differentiated from the skull, and the crests are less salient. No sutures between the various elements of the bullae can be seen, but a basisphenoid component was certainly present. As in Recent talpids, the bullae merge anteriorly with the side walls of the posterior narial passage but, in contrast to most of them, the basisphenoid and elements anterior to it are little if at all inflated or cancellous in the Proscalopinae. The basicranium in this area bears a slight but notable median crest that runs forward to about the level of the Eustachian openings. A similar but smaller crest can be seen in *Scalopus*, and in *Desmana* this crest is slightly larger. The external auditory meatus in *P. tertius* is a large opening, larger than in *Scalopus*. It is broken in the other fossil specimens. The foramen ovale can be seen in *P. secundus* in the usual position. Its large size suggests that it also gave passage to the tendon of M. tensor tympani, as in the chrysochlorids and smaller moles. It may also have housed a vein. The limits of the foramen rotundum cannot be determined, but it is anterior to the foramen ovale and in the usual position. The Eustachian openings are rather large and oval shaped, directed almost immediately ventrally. The openings are larger than any observed in chrysochlorids. Placed slightly lateral and posterior to the external

auditory meatus is the stylomastoid foramen, and postero-medial to it is the hyoidean vagina. The two are separated from the external auditory meatus by a low bar of bone. Conditions here are much as in the chrysochlorids. In Recent talpids, such as *Scalopus*, the openings are situated postero-lateral to the carotid foramen, not antero-lateral to it as in the fossils. The hyoidean vagina is much more pronounced than in the Recent forms. There are two other noticeable depressions on either side of the skulls, postero-lateral to the carotid foramen. One is almost directly posterior to the hyoidean vagina, the other posterior to this but more medial. The latter depression is somewhat elongate transversely. The function of these depressions is unknown.

The glenoid fossa of *P. secundus* and *P. tertius* is a much more pronounced structure than in Recent talpids. It is wider transversely and deeper, more as in chrysochlorids. It differs from these forms in having a prominent, anteriorly placed dorsal lip. The postglenoid foramen is extremely small and is situated high on the posterior face of the glenoid fossa near its lateral extremity. It is somewhat less lateral in position in the chrysochlorids, where it is on the medial face of the fossa and more nearly dorsal to the external auditory meatus. The usual condition in Recent talpids is for the foramen to be situated ventral to the posterior wall of the fossa, immediately dorsal to the anterior crus of the tympanic.

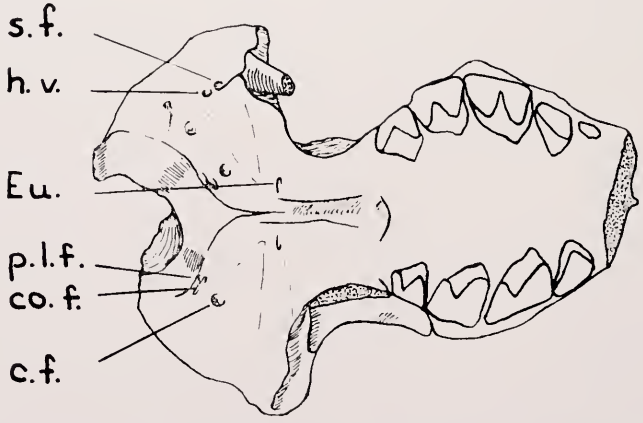

Fig. 1. Diagram of the basicranial region of *Proscalops tertius*. Stippled areas represent broken parts of skull. x3. Abbreviations: c.f., carotid foramen; co.f., condylar foramen; Eu., Eustachian opening; h.v., hyoidean vagina; p.l.f., posterior lacerate foramen; s.f., stylomastoid foramen.

The lower jaw

Rami are known in *Proscalops tertius*, *P. miocaenus* and *Oligoscalops*. These are slender and relatively uniform in depth. The rami of *Oligoscalops* show a slight bowing down below P_4-M_1, corresponding to the flexure in the upper tooth row. This bowing down is unlike anything seen in other talpids or in chrysochlorids. The symphysis was evidently elongate but weak. This is suggested by the rugose area on one of the rami of *Oligoscalops,* which extends posteriorly to P_4. In this respect the Proscalopinae do not differ from most talpids. The mental foramen, a single opening, is preserved only in *Oligoscalops,* where it is situated below P_3.

The posterior portion of the ramus is most completely preserved in *P. miocaenus* and the description is based on this specimen. The coronoid process rises at right angles to the main body of the ramus and, although incomplete at the tip, does not seem to curve posteriorly. It is not as narrow as in Recent talpids, and the posterior border, as in *Mogera*, has a forward slope. The condyle is wider than in Recent forms and is situated on a long stout neck. The angular process is short, stout and wide and leaves the body of the ramus at a lower level than in Recent talpids. In *Oligoscalops*, so far as can be told from the material, it is possible that the angle may have left the ramus at a somewhat higher level. The angle is not dorso-ventrally compressed as in *Uropsilus*. In comparison with the chrysochlorids, the proscalopine ramus is more slender. In the African forms, with the exception of the large *Chrysospalax*, the coronoid process is greatly reduced. The condyle is similar in inclination and in the structure of the neck, but the articular surface in the Proscalopinae faces essentially posteriorly whereas this surface in the chrysochlorids faces almost entirely dorsally. The angle of the chrysochlorids differs in being deeper and more compressed as well as projecting well below the horizontal ramus. The two groups are very distinct in this region.

The dentition

The diagnostic characters of the dentition of the members of the subfamily have been given in the taxonomic section. A more detailed treatment of the dentition and a brief comparison with Recent forms follow.

Upper dentition. In both *Oligoscalops* and *Proscalops secundus* the first incisor is enlarged and is flanked by two other small apparently conical incisors. I^3 is smaller than I^2 in *P. secondus;* these teeth are broken and represented only by the roots in

Oligoscalops. The canine is simple and conical in both specimens. It is larger than I^{2-3} in *P. secundus* and larger than the first premolar in *Oligoscalops*. All the incisors, canines and anterior premolars are separated from each other by diastemata. The premolar series consists of three teeth,[2] interpreted as $P^{1,3-4}$. In *Oligoscalops*, P^3 is laterally compressed, has a partially divided root, and is in contact with P^4. In *P. miocaenus* the two anterior premolars are badly worn. P^3 is not laterally compressed as in *Oligoscalops* and has one root. A diastema separates P^3 and P^4 in all species of *Proscalops*. In *P. secundus*, $P^{1,3}$ are simple, conical and single-rooted teeth. P^3 is present on the left side of *P. tertius* and agrees in form with that of *P. secundus*. These teeth are not known in *Mesoscalops*.

P^4 differs in the several species. In *Oligoscalops*, although worn, it consists of a large labial paracone with a parastylar area and a small conical lingual cusp. The latter cusp has a slightly pinched appearance and is directed posteriorly. In all the species of *Proscalops* and in *Mesoscalops*, P^4 lacks the parastylar area. In *P. miocaenus*, both the tooth as a whole and the lingual cusp are relatively larger than in *Oligoscalops*; again, the lingual cusp is directed posteriorly. P^4 of *P. tertius* is larger still and also has the essentially conical lingual cusp directed posteriorly. A change in P^4 becomes evident in *P. secundus*. In this species the lingual cusp has broadened and is more shelf-like in shape. It is also directed more medially than posteriorly, although no part of the lingual cusp extends anterior to the blade-like paracone. In *Mesoscalops* the antero-posterior broadening of the lingual cusp is carried further; it is here distinctly shelf-like. The lingual cusp extends slightly anterior to the paracone, although still directed essentially medially; it shows a partial division and the margin bears irregularities in the form of swellings. These are also present but are less numerous in *P. secundus*. One specimen of *Mesoscalops* exhibits a small cuspule on the posterior side of the labial cusp. In *Oligoscalops* and the species of *Proscalops* the tooth has three roots, two labial and one lingual. In *Mesoscalops* the roots have fused, but traces of the original divisions remain.

M^1 in *Oligoscalops* is triangular in general outline, with the protocone directed anteriorly. The hypocone is rudimentary, a mere protuberance labial and posterior to the protocone. The blade-like paracone is smaller than the V-shaped metacone. In *P. miocaenus* the tooth is generally similar, although the hypocone is somewhat better developed and the lingual portion of

[2] The premolar series might be $P^{1-2,4}$ by analogy with *Uropsilus*.

the tooth therefore somewhat broader. A rudimentary protostyle is present. Para- and metacones are similar to those of *Oligoscalops*. In *P. tertius* the hypocone is well developed. There is a small but distinct protostyle anterior to the protocone, and a minute hypostyle posterior to the hypocone. The protocone is directed somewhat more medially than in the earlier forms. The paracone is again smaller and more blade-like than the metacone. *P. secundus* continues the trend toward a squaring up of the outline of the tooth. The lingual shelf is wider, and the hypocone and protostyle better developed. The paracone is slightly more V-shaped than in earlier forms, and there is a small distinct parastyle. A metastyle is also present. M^1 of *Mesoscalops* has the protocone and hypocone more nearly equal in size, and lacks a protostyle, which gives a distinctly square appearance to the tooth. The para- and metacones resemble those of *P. tertius*, rather than those of *P. secundus*. Both the parastyles and metastyles are present.

M^2 of *Oligoscalops* and *P. miocaenus* are again similar, although that of the latter is larger and has a more pronounced protocone and parastyle; a metastyle is lacking. In both, the paracone and metacone are V-shaped. *P. tertius* is similar in general, again enlarging the lingual portion of the tooth by a well developed hypocone. It also has a parastyle, but no distinct metastyle. The tooth is essentially square, with paracones and metacones subequal in size. *P. secundus* is very similar, possessing a slightly more distinct parastyle and a rudimentary metastyle. In *Mesoscalops* the protostyle is less distinct, due to the equalization of the protocone and hypocone. A parastyle is present, but the metastyle is incorporated in the crest from the metacone.

M^3 in *Oligoscalops* and *P. miocaenus* is distinctly triangular, with the protocone directly lingual to the paracone. The hypocone is rudimentary in *Oligoscalops*, absent in *P. miocaenus*. There are no distinct stylar cusps in either form. This tooth, in both, is antero-posteriorly compressed, slightly less so in *Oligoscalops*. The posterior margin of the tooth is formed by the blade-like metacone. M^3 of *P. tertius* is similar although larger. The hypocone, however, is clearly present and lingual to the metacone which again forms the posterior margin of the tooth. A protostyle is suggested by a slight swelling. *P. secundus* has a wider lingual area with a distinct hypocone and protostyle. The metacone still forms the posterior margin of the tooth, although on RM^3 there is a minute cuspule posterior to the metacone. A

parastyle is present but there is no distinct metastyle. In *Mesoscalops* the hypocone is small and rather variable in shape, and the protostyle is very poorly developed. No distinct stylar cusps are seen. In all the specimens, M^3 is the smallest of the molars.

All the upper molars have three roots, two labial and one lingual. In *Mesoscalops* the lingual root is stouter and longer than the labial roots. The same is suggested for the others. In all, the protocone acquires a decidedly pinched appearance with wear, but the degree of pinching is not diagnostic.

Lower dentition. The incisors, canines and anterior premolars in *Oligoscalops*, the only form in which these teeth are known, are all broken or badly worn. The Kansas specimen suggests that the canine and P_1 and P_3 were simple, conical and single rooted. P_4 is laterally compressed and two rooted. In M_1 the talonid is wider than the trigonid, judging from the fragments that remain, and the opposite is true of M_2. A small anterior cuspule is preserved at the base of the paraconid of RM_2. In M_3 the trigonid is wider than the talonid. The relative sizes of the cusps on the molars cannot be determined, due to breakage. Matthew (1909, pl. 49) figures a right ramus of the type of *P. miocaenus*[3] in which the relative trigonid-talonid widths are as in *Oligoscalops*. The metaconid of M_2 is larger than either the paraconid or the entoconid. An anterior lingual basal cuspule is present in M_3. P_4 of this specimen has a small heel, but is essentially conical and apparently two rooted. P_3 is simple, conical and single rooted. All the left lower molars of *P. tertius* are known. In M_1 the trigonid is narrower than the talonid. The paraconid and metaconid diverge more than in M^{2-3}, and a small posterior cingular cuspule and a slight swelling on the lingual face of the paraconid are preserved. In M_2 the trigonid is wider than the talonid. The metaconid is stout with a rudimentary metastylid; there are both antero-internal and postero-internal cuspules. In M_3 the trigonid is again wider than the talonid. There is only an antero-internal cuspule. The lower dentition of *P. secundus* is unknown. M_1 of *Mesoscalops* has the trigonid narrower than the talonid, with the paraconid and metaconid widely divergent. A small postero-internal cuspule is present. M_2 has a metastylid, even more distinct than that in *P. tertius*, as well as antero-internal and postero-internal cuspules. The trigonid is equal in width to the talonid. M_3 has a simple metaconid and both antero- and postero-internal cuspules. The trigonid is wider than the talonid.

[3] This part of the type was not included in the material sent to me for study.

Comparison with Recent forms

Although the teeth of the Proscalopinae are talpid-like, a brief comparison with Recent forms is desirable. Most of the Recent talpids have three incisors, the first enlarged, the second and third decreasing in size. *Condylura*, however, has a large caniniform second incisor, larger than either I^1 or the canine. *Uropsilus*, apparently with only two incisors, possesses an enlarged I^2, but it is lower than I^1. In *Scalopus* the second and third incisors are minute and placed very close together. The second incisor is separated from the very large I^1 by a large diastema in *Desmana*. The canines in all but *Talpa* and *Mogera*, where they are large, are only slightly larger than the second or third incisor or the first premolar, as in the Proscalopinae. *Scalopus* and *Condylura* are the only Recent forms with a reduced premolar series. In *Uropsilus* P^3 is either present or absent; where present it is greatly reduced.[4] P^2 in this form is larger than both P^1 and P^3. P^4 shows the greatest difference between the Recent and fossil forms. *Condylura*, *Parascalops*, *Mogera*, *Neurotrichus*, and *Talpa* all have a small basal cusp anterior to the paracone. The lingual cusp in these forms is extremely small. The general structure of P^4 of *Oligoscalops* shows some similarity to these five genera. Both the anterior basal cusp and the lingual cusp are essentially lacking in *Scapanus* and *Scalopus*. P^4 of *Uropsilus* is more similar to most of the Proscalopinae than other talpids, but has a slight anterior cingulum not unlike *Desmana*. The lingual portion of the molars is narrower and lacks the hypocone development of the later Proscalopinae in all except *Neurotrichus*, *Parascalops*, *Uropsilus* and the members of the Desmaninae. In these forms the wider lingual portion does not show any pinching of the protocone, and the paracone and metacone of M^1 in *Neurotrichus* are much simpler than in the fossils. The position of the protostyle in *Desmana* is very different than in the Proscalopinae. In all Recent talpids, excepting *Scalopus* in which they are essentially lacking, the stylar cusps are more distinct than in the fossils. In the lower dentition, *Talpa*, *Mogera*, and *Condylura* have two-rooted premolar teeth. *Parascalops* and *Condylura* are the only Recent talpids that have metastylids on the molars. Although antero- and postero-internal cuspules are generally present, in no case do they connect with cingula as in the Proscalopinae.

[4] In three of four specimens examined, P^3 was present, although it was most greatly reduced in a male skull. The one skull lacking P^3 was also a male. Cabrera's dental formula is thus incorrect and should read for the upper dentition either $I^2\ C^1\ P^4\ M^3$ or $I^3\ C^1\ P^3\ M^3$, not $I^2\ C^1\ P^3\ M^3$ as given (Cabrera, 1925, Genera Mammalium, vol. 2, Insectivora, Galeopithecia).

Cingula are usually lacking, except in *Uropsilus* and some of the Desmaninae.

Further comparison between the Proscalopinae and Recent talpids in the dentition seems unnecessary; the extinct forms clearly differ from the living in various characters and combinations of characters. No comparison with the zalambdodont chrysochlorids is required.

Arctoryctes-Cryptoryctes and the Proscalopinae

It has been suggested by Matthew (1928) and by Schlaikjer (1933) that the humeri described as *Arctoryctes* may belong to the *Proscalops* group. This suggestion must now be considered.

Two points tend to support such an association. First, both skulls and humeri have talpid characters, yet neither are typically talpid. (The humeri, of course, are very different from those of the chrysochlorids.) Second, the published geologic and geographic ranges of the Proscalopinae and the *Arctoryctes* group overlap (see Table II).

Table II

	Oligocene			Miocene	
	Early	Middle	Late	Early	Middle
Cryptoryctes kayi	Montana				
Cryptoryctes sp.?	Colorado*				
Arctoryctes terrenus			S. Dakota		
Arctoryctes galbreathi		Montana Colorado			
Arctoryctes sp.?	Nebraska				Wyoming**
Oligoscalops whitmanensis		Wyoming Colorado			
Proscalops miocaenus			Colorado		
Proscalops tertius			S. Dakota†		
Proscalops secundus				S. Dakota	
Mesoscalops scopelotemos					Wyoming

* Recorded, but lost in the field.
** Species not identified. (Reed, C. A., pers. comm., 1961).
† Exact horizon uncertain.

A comparison of the skull length/humerus length ratio has been made for modern talpids, for a chrysochlorid, and for selected proscalopine skulls and arctorycline humeri. In two cases, skull material and humeri are known from the same horizon and locality: *Oligoscalops whitmanensis* (K.U.M.V.P. no. 8143) and *Arctorycles galbreathi* (K.U.M.V.P. nos. 9837-9839); and *Mesoscalops scopelotemos* and an unidentified species of *Arctorycles*. In the first case, unfortunately, the two best preserved humeri are broken, and the measurements, kindly supplied by C. A. Reed, are only approximate. No measurements are available for the humeri found with *Mesoscalops scopelotemos*. There is a fair correspondence in time in one other case, that of *Proscalops secundus* and *Arctorycles terrenus;* the former is probably from a somewhat earlier horizon in the Miocene of South Dakota than the latter. All other occurrences are rather widely separated in time or space. There is no known proscalopine that could correspond to the small *Cryptorycles kayi*. The ratios (Table III) of *Oligoscalops whitmanensis/Arctorycles galbreathi* and *Proscalops secundus/Arctorycles terrenus* do not differ greatly from those of certain talpids but do differ from that of the only chrysochlorid available for comparison. These ratios at least suggest that association is not impossible.

TABLE III

specimen		skull/humerus ratio	remarks
Scapanus		229%	from Reed, 1954
Condylura		245%	" " "
Neurotrichus		304%	" " " (long skull)
Chrysochloris stuhlmani		180%	
Oligoscalops whitmanensis	skull	252-256%	based on estimated humeri lengths
Arctorycles galbreathi	humerus		
Proscalops secundus	skull	245%	slight difference in age
Arctorycles terrenus	humerus		

Although not impossible, the association of the skulls and humeri is, of course, very far from proven. A typical talpid humerus is known from the mid-Oligocene Cedar Creek member of Colorado (Galbreath 1953), the same deposit that has yielded specimens of *Oligoscalops whitmanensis* and *Arctoryctes galbreathi*. The earliest non-proscalopine North American talpid is *Domninoides;* two species of this genus are known from the earlier Miocene, one of them from beds just below those containing *Proscalops secundus* (Macdonald, pers. comm.). I have seen typical talpid humeri from a deposit that has yielded remains of *Domninoides* ("Valentine formation," Fort Niobrara locality) and strongly suspect that these humeri are referable to that genus. It seems likely that the Cedar Creek talpid humerus represents some otherwise unrecorded member of the family, but the possibility that it is referable to *Oligoscalops* should not be ignored — nor can the possibility be ignored that the *Arctoryctes-Cryptoryctes* humeri may be referable to some other group altogether. Only the fortunate discovery of proscalopine cranial or dental material in unmistakable association with arctoryctine humeri will settle the question.

After this study was completed, Russell (1960) suggested that the arctoryctine humeri may belong to *Micropternodus* and related forms, since a humerus, identified by C. A. Reed as *Cryptoryctes*, occurs at a locality that has yielded "*Kentrogomphios*" (= *Micropternodus*). Furthermore, if the skull proportions of *Micropternodus* are similar to those of talpids, the skull/humerus ratio of *Micropternodus* and *Cryptoryctes* (248%) is much closer to those of talpids than to those of epoicotherids or apternodontines, again suggesting a possible relationship between *Micropternodus* and *Cryptoryctes*.

This ratio is not very different from that obtained by comparing proscalopine skulls and arctoryctine humeri. However, as the evidence supporting the association of the humeri with either the Proscalopinae or the *Micropternodus* group is no more than circumstantial at best, it is not possible to draw any conclusions at this time.

CONCLUSIONS

The morphological characters of the skull obviously unite the proscalopine species and clearly separate them from other talpids. As regards intergroup relationships, it can be stated that *Oligoscalops*, the earliest known form, can be easily distinguished

from the rest of the subfamily on the characters of P^3 and P^4, although the overall cusp pattern and the structure of the molars are not very different from *Proscalops*. Within the genus *Proscalops* there are certain trends in the evolution of the dentition that may easily be seen. There is a tendency to broaden the lingual portion of the upper molars and P^4, with a general squaring of the outline of these teeth. In the lower molars there is a progressive complication of the teeth by the addition of antero- and postero-internal cuspules and the development of a metastylid. *Mesoscalops*, the latest known form, while similar in the general pattern of the lower molars, has modified the upper molars by eliminating the protostyles. P^4 of this form differs in having incipient division of the lingual cusp as well as fusion of the roots. This genus could, however, have been derived from a form not unlike *P. secundus*. The mutual relationships within the subfamily appear to be as in Figure 2.

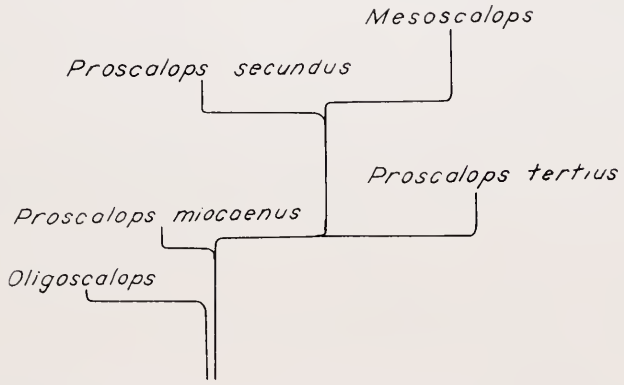

Fig. 2. Diagrammatic representation of the relationship of the known members of the Proscalopinae.

The Proscalopinae are very different from all other talpids so far as the characters of the skull are concerned. In this the group differs more from the other talpid subfamilies than these subfamilies do from each other. This suggests that it might be more proper to group all other moles, with the exception of the Desmaninae, in one subfamily. Our ignorance of the family is such, however, that I do not take this step. If the curious arctoryctine humeri should prove to be referable to the proscalopines, the combination of cranial and humeral characters would certainly warrant the erection of a new family for the Proscalopinae, as Matthew suspected.

It has been shown that there is a remarkable parallelism between the proscalopines and the chrysochlorids. This is particularly evident in the premaxillary region, the squamosal flange, seen particularly in *P. secundus*, and the general structure of the basicranial region. The fact that these peculiar fossorial adaptations have arisen more than once in the Insectivora removes some of the uniqueness of the chrysochlorids.

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PLATES

Plate 1

Fig. 1. *Oligoscalops whitmanensis*, C.N.H.M. P25800, ventral view
Fig. 2. *O. whitmanensis*, dorsal view
Fig. 3. *O. whitmanensis*, left profile
Figs 1-3 approx. 2.5x
Fig. 4. *Proscalops tertius*, A.M.N.H. 19420, stereoscopic pair, crown view, approx. 4.5x
Fig. 5. *Oligoscalops whitmanensis*, K.U.M.V.P. 8143, stereoscopic pair, crown view, approx. 4.5x
Fig. 6. *Proscalops tertius*, ventral view
Fig. 7. *P. tertius*, left profile
Figs. 6 and 7 approx. 2.5x

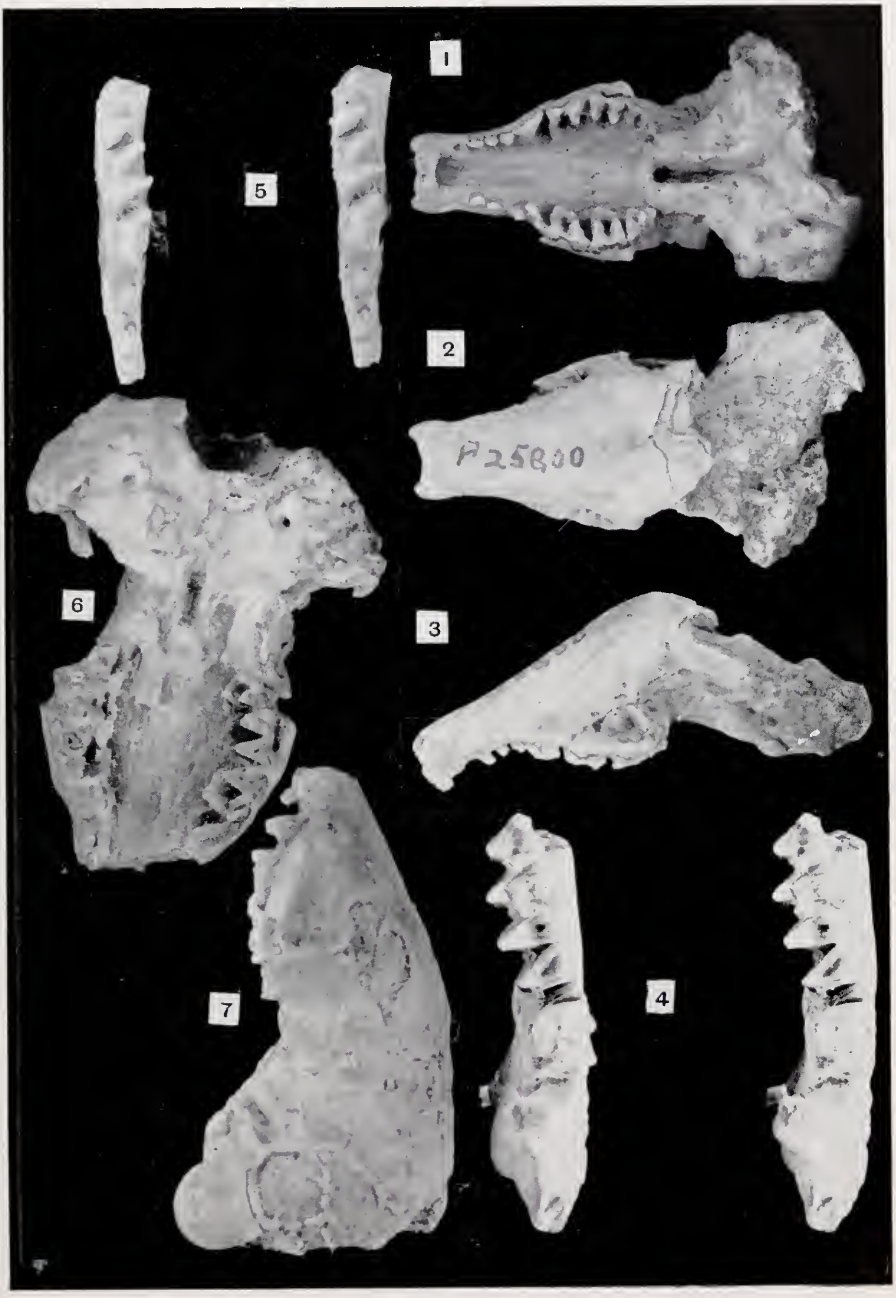

PLATE 1

Plate 2

Fig. 8. *Proscalops secundus*, A.M.N.H. 13798, ventral view
Fig. 9. *P. secundus*, dorsal view
Fig. 10. *P. secundus*, right profile
Figs. 8-10 approx. 3x
Fig. 11. *Oligoscalops whitmanensis*, C.N.H.M. P25800, left ramus, approx. 4.3x
Fig. 12. *Proscalops miocaenus*, A.M.N.H. 8949a, right profile, approx. 2.5x
Fig. 13. *Oligoscalops whitmanensis*, C.N.H.M. P25800, stereoscopic pair, crown view, approx. 4x

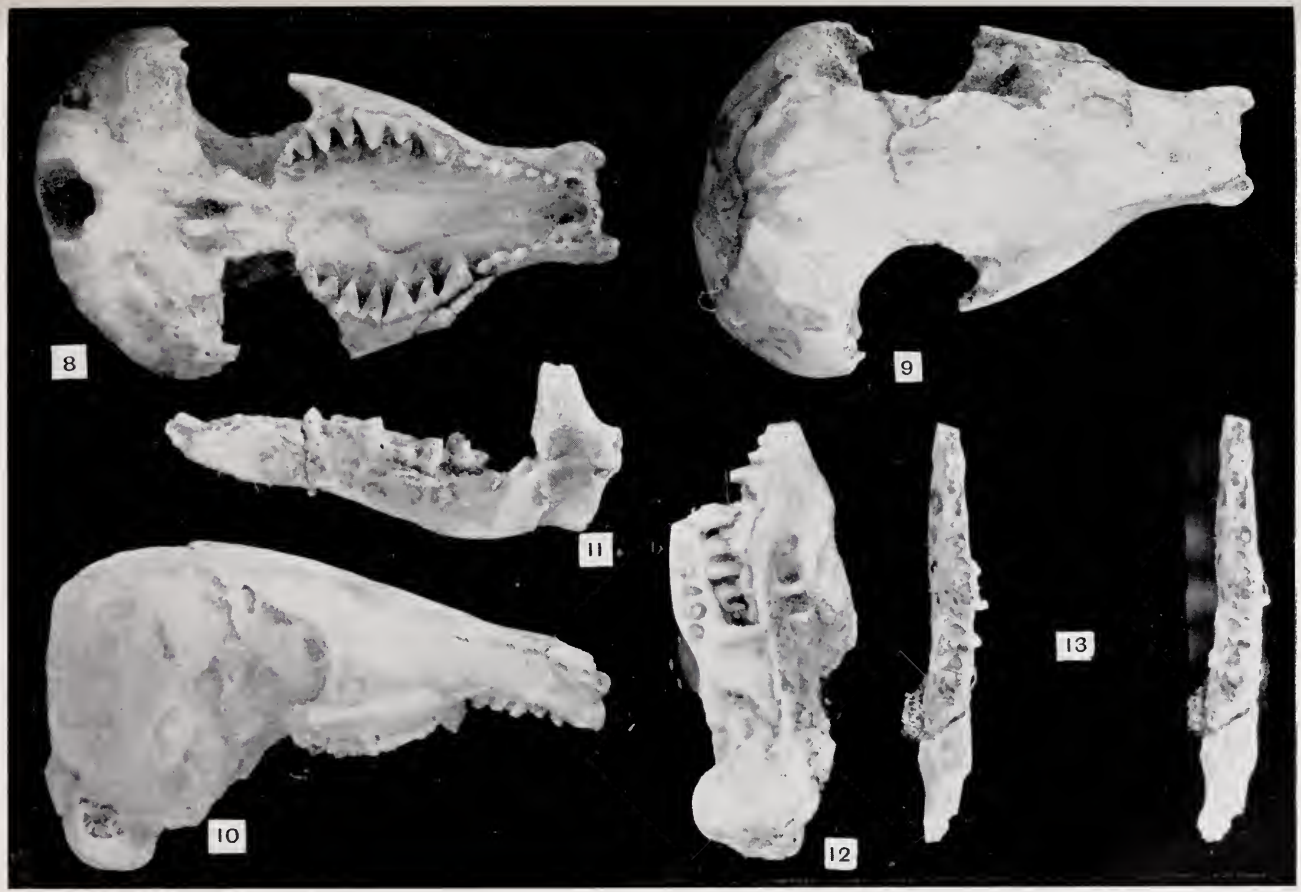

PLATE 2

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